

COMPARATIVE REPRODUCTIVE BIOLOGY OF THE TASMANIAN
FRESHWATER CRAYFISHES *Astacopsis gouldi* CLARK, *Astacopsis franklinii*,
GRAY AND *Parastacoides tasmanicus* CLARK (DECAPODA: PARASTACIDAE)

by

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Submitted in fulfilment of the requirements

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This thesis contains no material which has been accepted for the award of any other higher degree or graduate diploma in any tertiary institution, and to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

A handwritten signature in black ink, reading "Premysl Hamr". The script is cursive and fluid, with the first name "Premysl" and the last name "Hamr" clearly distinguishable.

Přemysl Hamr, January 1990.



" The northern Crayfish grows to nearly two feet in length, and may scale eight or nine pounds; it is dark green in colour, and studded on the claws and gill covers with blunt tubercles; the claws of the larger specimens are formidable weapons about the size of a man's hand. We obtained the largest specimens from Muddy Creek, a small rivulet that one could easily step across, and it seemed extraordinary to fish these huge monsters out of little pools in which one would expect to find nothing larger than a minnow. "

Geoffrey Smith, 1909

in "A Naturalist in Tasmania"

Frontispiece: *Astacopsis gouldi* Clark (immature crayfish, life size).

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ABSTRACT

The reproductive biology and life history of the Tasmanian freshwater crayfishes in the endemic genera *Astacopsis* and *Parastacoides* were studied in the field and laboratory from April 1985 to May 1987.

A. gouldi and *A. franklinii* are open water species associated with riverine and lacustrine habitats from highlands to coastal plains. The burrowing, semi-terrestrial *P. tasmanicus* occurs in wet heathlands, water courses and highland lakes in the wetter cooler, western half of the state.

The three species were studied in representative, relatively undisturbed habitats. The habitats of all three species were typified by low water temperatures, high rainfall and fluctuating water levels.

Reproductive morphology and anatomy of *Astacopsis* and *Parastacoides* was described in detail. Male and female gonads differ from those of northern hemisphere crayfishes, resembling anatomically the gonads of the Palinuridae. The male gonopores show considerable complexity and variation among genera. Female genitalia undergo significant changes in morphology at the onset of sexual maturity.

Sexual dimorphism is developed to a greater degree in *Astacopsis* than in *Parastacoides*. Secondary sexual characters are more numerous in females of both genera and perform important functions in spawning and incubation of eggs.

Data on seasonal reproduction, growth, population structure and density were obtained from regular sampling and mark recapture programs. Size at maturity and reproductive condition were determined by changes in reproductive morphology and gonad condition.

In both genera males reach sexual maturity at a smaller size than females. Females, upon reaching maturity, exhibit a biennial breeding and molting cycle which is a unique strategy, apparently a result of the cooler climate conditions in Tasmania. In *Astacopsis*, mating and spawning take place in autumn, eggs are carried over winter, hatch mid to late the following summer and young remain attached until late summer to early autumn. *Parastacoides* mates and spawns in autumn, eggs are carried over winter, hatch early the following summer and postlarvae remain attached until mid summer.

The larval development and morphology of *Astacopsis* and *Parastacoides*

was described. Marked differences between the two genera were found and the "primitive" larval development of *Astacopsis* differed significantly from that described for other freshwater crayfishes.

Growth rates, although faster in juveniles, are relatively slow in adults of both genera. In reproductive adults of both sexes, molting frequency is low (apparently biennial). This results in maturity being reached late and at a relatively large size as well as in overall longer life spans as compared to most other freshwater crayfishes.

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CHAPTER 1 GENERAL INTRODUCTION

Freshwater crayfishes (Superfamilies Astacoidea and Parastacoidea) make up a significant component of the freshwater fauna of all continents except for Africa. Crayfishes found in the Northern Hemisphere belong to two families: 1. the Astacidae of Europe, western North America and western Asia; and 2. the Cambaridae of central and eastern North America, Middle America and eastern Asia. All crayfishes found in the Southern Hemisphere belong to one family: the Parastacidae.

The family Parastacidae, Huxley 1879, which ranges from the tropics to the cool temperate subantarctic regions, contains the thirteen genera of crayfishes listed in Table 1.1. Australia's crayfish fauna can be seen to be particularly rich containing nine of the thirteen known genera mentioned above. Tasmania, although small in area when compared to the rest of the continent, has representatives of four of these genera (*Engaeus*, *Geocharax*, *Parastacoides* and *Astacopsis*) with *Astacopsis* and *Parastacoides* being endemic.

The members of the genus *Astacopsis*, which include the world's largest freshwater crayfish (and therefore invertebrate) species, are associated with riverine and lacustrine habitats throughout Tasmania (Swain *et al.*, 1982). Taxonomically and ecologically their closest relatives are the crayfishes of the genera *Euastacus* and *Astacoides* (Hobbs, 1987 & 1988; Riek, 1972; Patak & Baldwin, 1984). The genus was first erected by Huxley in 1878 but earlier accounts and descriptions of crayfish now placed in this genus are available (Gray, 1845; Gould, 1870). Perhaps the earliest representation of *Astacopsis* is a painting made in 1832 by the convict artist William Buellow Gould in his "Book of Fishes" (Fig.1.1). The pictured crayfish is clearly identifiable as the large western form of *A. franklinii*, probably from the lower reaches of the Gordon River.

The existence of several Tasmanian varieties of crayfishes within the genus was recognized by Smith (1909A, 1912) but he retained a single specific name, *A. franklinii*, for all Tasmanian members of the genus. Clark (1936) separated the Australian and Tasmanian members of the genus, assigning the former to a new genus *Euastacus* while reserving *Astacopsis* for the latter. At the same time she revised *Astacopsis* adding two new species: *A. gouldi* (from northern Tasmania) and *A. tricornis* (from Lake St. Clair region). *A. franklinii* was retained and used for the smaller *Astacopsis* from the Launceston and Hobart regions. Riek (1969)

TABLE 1.1: Family Parastacidae: Genera and distribution

<u>Genus</u>	<u>Geographic region</u>	<u>Reference</u>
<i>Astacoides</i>	Madagascar	Hobbs,.1987
<i>Astacopsis</i>	Tasmania	Swain <i>et al.</i> , 1982
<i>Cherax</i>	Mainland Australia New Guinea	Riek, 1979 Holthuis, 1986
<i>Engaeus</i>	Mainland Australia Tasmania	Horwitz, 1986
<i>Engaewa</i>	Mainland Australia (Western Australia)	Riek, 1969
<i>Euastacus</i>	Mainland Australia	Morgan, 1986 & 1988
<i>Geocharax</i>	Mainland Australia Tasmania	Horwitz, 1986
<i>Gramastacus</i>	Mainland Australia	Riek, 1972
<i>Paranephrops</i>	New Zealand	Hopkins, 1970
<i>Parastacoides</i>	Tasmania	Sumner, 1978
<i>Parastacus</i>	South America	Riek, 1971
<i>Samastacus</i>	South America	Riek, 1971
<i>Tenuibranchiurus</i>	Mainland Australia	Riek, 1969

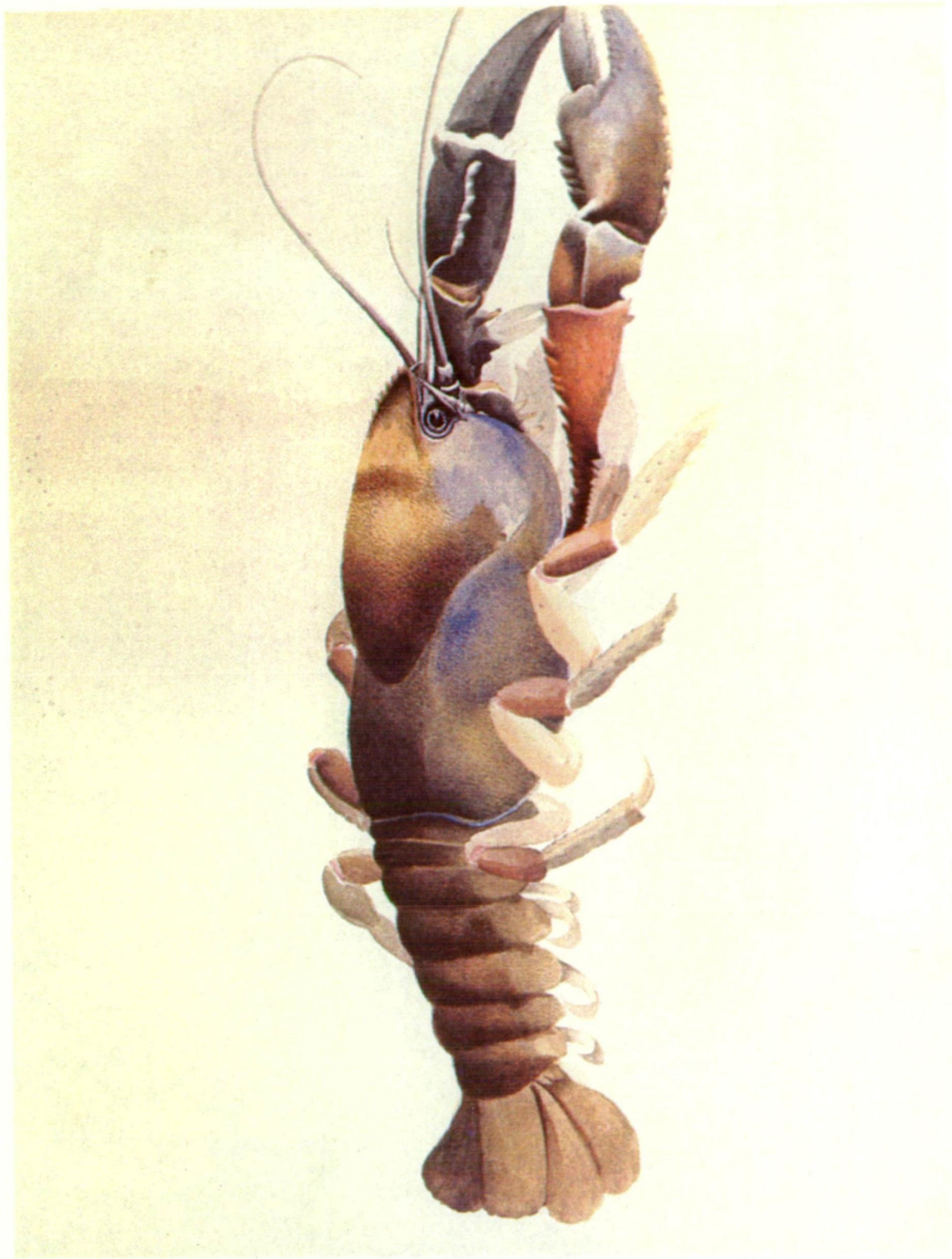


Figure 1.1 Study of *Astacopsis franklinii* (western form) from W.B. Gould's "Book of Fishes" (1832).

added another species, separating *A. franklinii* into *A. fluviatilis* (from southern Tasmania) and *A. franklinii* (from Northern Tasmania). Swain *et al.* (1982) revised the genus and reduced the number of species from four to two by including *A. fluviatilis* and *A. tricornis* within *A. franklinii*.

A. gouldi, the giant freshwater crayfish or "lobster", as it is called locally, is the world's largest known crayfish attaining weights of more than three kilograms (Smith 1909A & B; Lynch, 1967; Wells *et al.*, 1983; Hobbs, 1988). The species is restricted to the north of Tasmania where it can be found in streams, rivers and reservoirs draining into the Bass Strait as well as in the Arthur River system in the extreme north-west (Swain *et al.*, 1982).

A. gouldi appears to prefer cool water (less than 15 ° C), well-shaded by streamside vegetation (Forteath, 1985). It can be found in deep pools, sheltering under submerged rocks and logs as well as in shallower swift-running sections (Gould, 1870; Lynch, 1967). The diet of *A. gouldi* consists of semi-decayed wood, leaves and detritus (Gould, 1870; Forteath, 1985).

Its large size makes fishing for this crayfish a popular pastime for inhabitants of northern Tasmania and the resulting recreational fishery is controlled by the Inland Fisheries Commission under Tasmanian fisheries legislation. In addition the species is the subject of regular enquiries from aquaculturalists from Australia and overseas. Recently there has been concern from scientists and fishermen over the species' status (due to overfishing and habitat alteration) and this has led to a "vulnerable" listing in the International Union for the Conservation of Nature Invertebrate Red Data Book (Wells *et al.*, 1983). A recent study of the aquaculture potential of *A. gouldi* has found it "not a suitable animal for intensive farming" due to slow growth rates and intolerance of elevated temperature (Forteath, 1985).

A. franklinii is found throughout most of Tasmania (Swain *et al.*, 1982) in, or in association with, streams, rivers and lakes. Although generally smaller than *A. gouldi* it appears to vary greatly in size and spininess. In their reexamination of the various morphological characters, Swain *et al.* (1982) found that the variation in spininess and size had a geographical basis. It will be shown in Chapter 3 that this variation is in fact at least partly due to the occurrence of two distinct forms within *A. franklinii*. Apart from the above mentioned taxonomic literature and several comparative studies of exoskeleton calcification (Mills & Lake, 1976) and respiratory physiology (Swain *et al.*, 1987 & 1988) there is little information available on the

biology of this species.

The members of the genus *Parastacoides* are all small, generally semiterrestrial, burrowing crayfishes associated with wet heathlands, forests, rivers, streams and highland lakes throughout the wetter cooler, western half of Tasmania (Lake & Newcombe, 1975; Sumner, 1978; Richardson & Swain, 1980).

The phylogenetic relationship of *Parastacoides* to other Parastacidae is not clear. Riek (1972) thought it to be a branch of the *Cherax* lineage with *Paranephrops* being its closest relative, while more recently it has been shown that it may be more closely related to the *Astacopsis-Euastacus* lineage (Knott, 1975; Horwitz, 1986; Grouns & Richardson, 1989; Patak *et al.*, 1989).

In her taxonomic revision of Australian crayfishes, Clark (1936) erected the genus *Parastacoides* to accommodate *Astacus tasmanicus* Erichson 1846. She subsequently added two new species: *P. inermis* and *P. insignis* (Clark, 1939). Riek (1951) recognized yet another new species *P. setosimerus*, and subsequently described an additional three species: *P. leptomerus*, *P. sternalis* and *P. pulcher*, at the same time synonymizing *P. setosimerus* with *P. tasmanicus* (1967). In the most recent revision, Sumner (1978) concluded on the basis of numerical taxonomic procedures that the genus consists of a single species *P. tasmanicus*, made up of three subspecies: *P. t. tasmanicus*, *P. t. inermis* and *P. t. insignis*. The latest ecological, electrophoretic and morphological evidence shows however that the three subspecies should, in fact, be regarded as separate species (Richardson & Swain 1980; Grouns 1986), and there are several other new species to be described (Richardson, pers. comm.).

All crayfishes in the genus *Parastacoides* can be categorized as primary burrowers (Hobbs, 1981). *P. t. tasmanicus* is found in sedgeland and forest habitat in the west of Tasmania (Sumner, 1978; Grouns & Richardson, 1988). It reaches the highest densities in heath and sedgeland plains dominated by button grass (*Gymnoschoenus sphaerocephalus*) where it burrows into the wet podzol peat soils (Lake & Newcombe, 1975; Grouns & Richardson, 1988). These soils are characterized by relatively low temperatures, low pH, waterlogging and low nutrient levels (Bowman *et al.* 1986).

The burrows of *P. t. tasmanicus*, which have been described by Lake and Newcombe (1975) as well as Richardson and Swain (1980), range from simple, with a single entrance and one main underground chamber, to complex, with multiple

entrances and several chambers. They can all be classified as type 2 burrows, using the scheme proposed by Horwitz and Richardson (1988). Grown and Richardson (1988) found the burrows include blind, root-lined "feeding" chambers and that larger animals occupy larger burrows with a larger percentage of volume in feeding chambers. Richardson (1983) found that the burrows increased the aeration of the soil, thus encouraging rootlet and fungi growth and raising the soil respiration rate.

The diet of *P. t. tasmanicus* consists mainly of plant material such as roots and decomposing *Gymnoschoenus* leaf fragments, with animal matter making up only a small portion of total food consumed (Lake & Newcombe, 1975; Grown & Richardson, 1988). Grown and Richardson (1988) found that all categories of food varied seasonally. Less food was consumed during the winter months overall and animal material was present in the gut mainly in the summer months. They also found that the diets of adults and juveniles differed with respect to prey size and diversity, with juveniles consuming a greater amount and variety of smaller sized animal matter

P. t. tasmanicus appears well adapted to its burrowing lifestyle within its harsh environment which is characterized by low pH, extremes of temperatures, and ionic as well as oxygen deficiencies. Periodic desiccation of burrows may also occur during summer months. *P. t. tasmanicus* is tolerant of low pH, low oxygen levels, and has low water and ion loss (Fradd, 1979). It can survive out of water indefinitely at 100% relative humidity and adult individuals can tolerate desiccation over a wide range of relative humidities (Newcombe, 1970; Fradd, 1979). Swain *et al.* (1987) found that during hypoxia, the oxygen consumption, as well as the heart and scaphognathite beat rates, were lower in *P. t. tasmanicus* than in the stream-dwelling *A. franklinii*. Despite a reduction in gill number *P. t. tasmanicus* also has a significantly greater gill area and branchial volume per unit body size than *A. franklinii* (Swain *et al.*, 1988). *P. t. tasmanicus* has less exoskeletal calcium than *A. franklinii* but its distribution pattern is thought to be related to burrowing activity (Mills & Lake, 1976).

Little biological information is available for the other subspecies. Fradd (1979) considered *P. t. insignis* and *P. t. tasmanicus* very similar morphologically, ecologically and physiologically, while he thought *P. t. inermis* differed from the two at least ecologically. The habitats of the three "sub-species" were described by Richardson and Swain (1980) who found that *P. t. inermis* was found in two

disjunct habitats: under rocks in rainforest creeks and in drier, well-drained slopes in heathland; *P. t. tasmanicus* was found in waterlogged soil on sedgeland valley floors, while *P. t. insignis* occupied an intermediate habitat between the former two.

As little is known about the details of the life histories of Tasmanian Parastacidae, the principal aim of this study was to describe and compare their life cycles and in particular, their reproductive biology. The genera *Astacopsis* and *Parastacoides* were chosen because they are relatively widespread Tasmanian endemics, and, although they probably come from the same phylogenetic lineage, there should be some major differences in their life cycles because of the differences in their general biology: *A. gouldi* and *A. franklinii* are open water crayfish, living in rivers, lakes and streams, while *P. tasmanicus* is a burrowing crayfish, living in extensive flooded burrows. The reproductive biology of the two *Astacopsis* species should therefore be similar (because of very close phylogenetic relationship as well as similar lifestyle), while *Parastacoides* should show major differences due to its burrowing, semiterrestrial lifestyle in a habitat which is markedly different from that of *Astacopsis*. Furthermore, endemic Tasmanian crayfishes can be expected to have different life history strategies from most other Australian species, because of the climatic differences between Australia and Tasmania. Tasmania is characterized by much cooler and wetter conditions as well as shorter, cooler summers which ultimately result in a relatively short period available for growth and reproduction. Momot (1984) suggests that crayfishes living at high latitudes and in cooler environment may be expected to mature late in life, have a prolonged breeding cycle, many reproductive age groups and long life span. This study therefore sets out to investigate and characterize the reproductive biology of *Astacopsis* and *Parastacoides* and compare the results, in a broad sense, to the overall trends in freshwater crayfish reproductive strategies.

CHAPTER 2. GENERAL METHODS

2.1 Study site selection and monitoring

A major study site was selected for each of the three species studied. In addition periodic samples were taken at several minor sites for each species.

Astacopsis gouldi was studied intensively at the Inglis River near the township of Yolla in north west Tasmania (Fig. 2.1). This site was selected because, although subject to some recreational fishing, it appeared to support a reasonably dense population of a *A. gouldi*. Additional minor sampling sites for this species were Lilydale Falls in north east Tasmania, and Detention River, Big Creek, and Dip River in north west Tasmania (Fig. 2.1).

Astacopsis franklinii was studied intensively in Hobart Rivulet and its tributary Guy Fawkes Rivulet, two creeks on Mt Wellington in Hobart, south east Tasmania (Fig. 2.1). This site was selected because it appeared to support a reasonable number of *A. franklinii*. It was also easily accessible and thus could be sampled frequently. Additional minor sampling sites where *A. franklinii* was collected included Clarence Lagoon in the central highlands of Tasmania, Pelverata Falls in south east Tasmania and New Town Rivulet on Mt Wellington (Fig. 2.1).

Parastacoides tasmanicus was studied intensively on a buttongrass plain near Harlequin Hill in south west Tasmania (Fig. 2.1). This site was chosen because it supported a large population of *Parastacoides tasmanicus* and concurrent studies of the ecology of *Parastacoides* by other members of the Zoology Department were under way in this area. Additional sites included sedgeland near the Scotts Peak hydroelectric dam and an area near the Needles Range, both in the south west of Tasmania (Fig. 2.1).

In the course of this study other numerous collections were made throughout Tasmania to gain further information on the distribution and biology of the two genera studied (see Chapter 3).

Water temperature was monitored at each major study site using a maximum/minimum thermometer (in the case of *P. t. tasmanicus* the temperature was taken 30 cm down a burrow). Flow, water quality, precipitation, and air temperature data for the relevant period were obtained from the Rivers and Water Supply

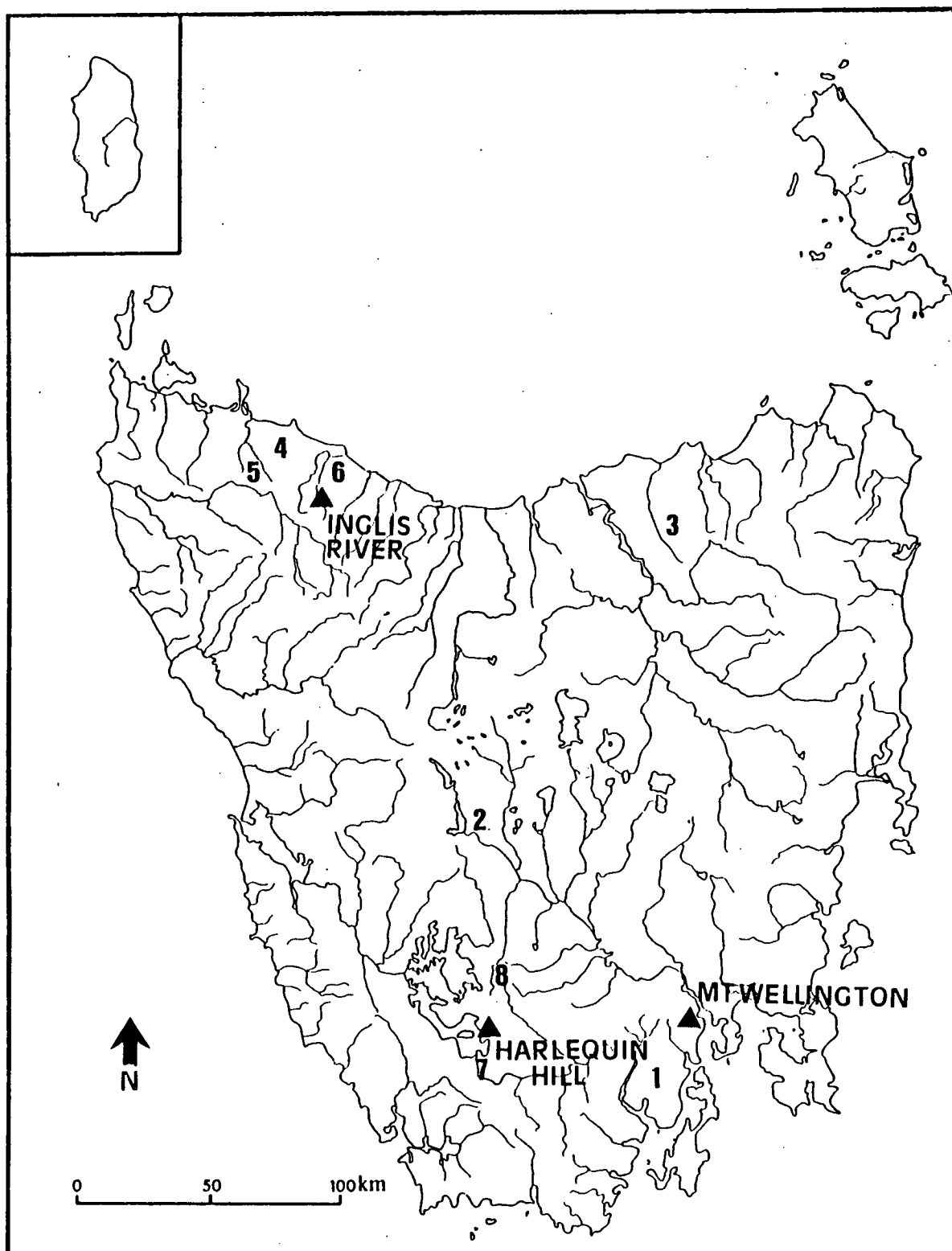


Figure 2.1 Location of sampling areas. Major sites are shown as triangles and minor sites are shown as numerals: 1. Pelverata Falls, 2. Clarence Lagoon, 3. Lilydale Falls, 4. Detention River, 5. Dip River, 6. Big Creek, 7. Scotts Peak, and 8. The Needles.

Commission and the Bureau of Meteorology in Hobart.

2.2 Duration of study and sampling frequency

Astacopsis gouldi: The Inglis River was visited monthly from November 1985 to May 1987. Two additional samples were taken in November 1987 and February 1988. Each collecting trip consisted of two to three days and nights of intensive trapping and hand collecting.

Astacopsis franklinii: Hobart and Guy Fawkes Rivulets were sampled several times each month from September 1985 to May 1987. Each sampling trip consisted of two to four hours of intensive crayfish collecting. Overall, 61 trips were made to Hobart Rivulet while Guy Fawkes Rivulet was visited 55 times.

Parastacoides t. tasmanicus: The Harlequin Hill site was sampled monthly from April 1985 to April 1987. Additional trips were made during the mating/spawning season to gain detailed information of reproductive activity. Each collecting trip consisted of two to three days of intensive burrow excavation. Overall the sampling area was visited on 31 occasions.

2.3 Capture methods

Astacopsis gouldi: Crayfish were captured primarily by drop nets (Fig. 2.2), single bait lines and monofilament "tangle" nets, baited with fresh fish pieces. All baited lines and nets were inspected periodically throughout the sampling period. Crayfish were also collected by hand, using snorkeling equipment and by turning over rocks and submerged logs. As the fishing methods and bag limit for this species are controlled, appropriate permits for the use of nets and the collection of large numbers of animals were obtained from The Tasmanian Inland Fisheries Commission.

Astacopsis franklinii: In Hobart, Guy Fawkes, New Town and Plover Rivulets crayfish were collected primarily by hand. Crayfish were caught when walking on the



Figure 2.2 Baited drop net, set in the Inglis River.

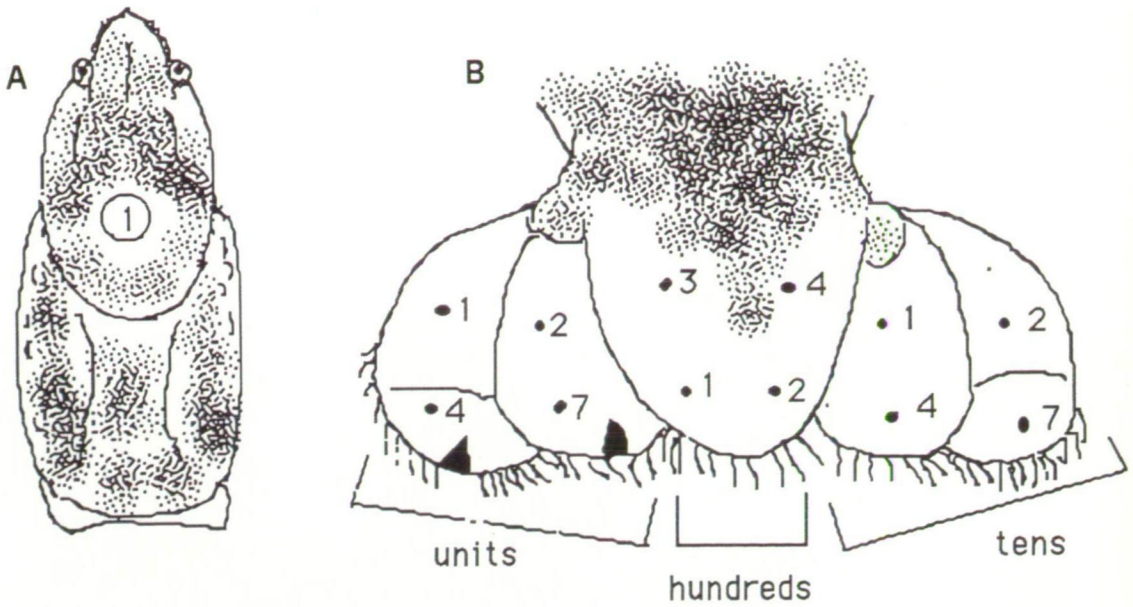


Figure 2.3 Marking system used for A. gouldi.

A. Number scratched on back of carapace.

B. Patterns of punctures and clips on tail fan.

stream bed and under rocks and logs. Some baited lines were used mostly over the summer months.

In Clarence Lagoon crayfish were collected from the lake bed using snorkeling equipment.

Other sites were sampled by hand or using baited nets. Appropriate permits were obtained from The Tasmanian Inland Fisheries Commission.

Parastacoides t. tasmanicus: Crayfish were collected by careful excavations of their burrow systems. Special care was taken to collect all crayfish in each burrow system. When large broods of small juveniles were present a representative sample was taken from each burrow. Burrow systems which were dug up were not resampled.

In the capture/recapture component of the sampling regime at the Harlequin Hill site crayfish were captured in pitfall traps. The traps and trapping methods were developed in conjunction with a study of the activity of *P. t. tasmanicus* by Dr. R. Swain of the the Zoology Department at the University of Tasmania. The traps consisted of plastic flower pots, sunk into the ground near burrow openings, into which crayfish fell during nocturnal activity on the surface. The trapping grid consisted of a rectangular area (20 x 25 meters) containing 250 traps which were checked early in the morning on each sampling day. Between sampling trips the traps were "disarmed" by inserting large twigs into each pot which any trapped animals could use as ladders to escape.

Appropriate permits for collection of all crayfish species were obtained from The Tasmanian Inland Fisheries Commission as well as The Lands and Parks Department.

2.4 Sample treatment

All crayfish captured were checked for molting and reproductive condition. The location of capture was also noted, ie: on stream bed or in a burrow in a particular section of sampling area.

Carapace length (CPL = rostrum tip to back edge of carapace) was used as a standard length measure and was recorded to the nearest tenth of a millimeter with Vernier calipers for all crayfish captured. Because some studies of the Parastacidae

have used ocular carapace length (OCL = posterior edge of orbit to back edge of carapace) conversion factors for the three major species are given below:

A. gouldi: $CPL = OCL \times 1.20$

A. franklinii: $CPL = OCL \times 1.16$

P. t. tasmanicus: $CPL = OCL \times 1.13$

In *Astacopsis gouldi* additional morphometrics were measured in the field to compensate for the small number preserved for laboratory analysis. Crayfish were then marked (see below) and released at the location of capture. A portion of the samples was preserved for laboratory analysis. Only few *A. gouldi* were preserved due to the species' vulnerable status. Similarly, only small numbers of *A. franklinii* adults from Mt Wellington were preserved because of the possibility of disrupting the relatively small adult population by excessive sacrifice. The preserved crayfish were fixed in 10% formalin immediately in the field and then transferred to 70% alcohol after 12 hours. A number of live animals was taken back to the laboratory to be used in molting and reproductive biology experiments.

2.5 Marking System

Astacopsis gouldi: All crayfish captured, excepting preserved and experimental individuals, were marked and released. From November 1985 to February 1986 crayfish were marked with a clip in the tail fan corresponding to month of capture (Fig. 2.3B.). From March 1986 to February 1988 crayfish were marked with tail punctures corresponding to individual numbers (after Lake and Sokol, 1986) (Fig. 2.3B.). The individual's number was also scratched out on the dorsal side of the carapace for quick recognition of unmolted individuals (Fig. 2.3A.).

Astacopsis franklinii: All crayfish captured in Hobart and Guy Fawkes Rivulets, excepting preserved and experimental individuals, were marked and released (crayfish captured at other sites were not marked). Because of relatively low recapture rates crayfish were marked only with a series of clips and punctures of the tail fan, abdomen and carapace corresponding to the month of capture (Fig. 2.4A.).

Parastacoides tasmanicus: Only crayfish captured in the pitfall traps at Harlequin Hill

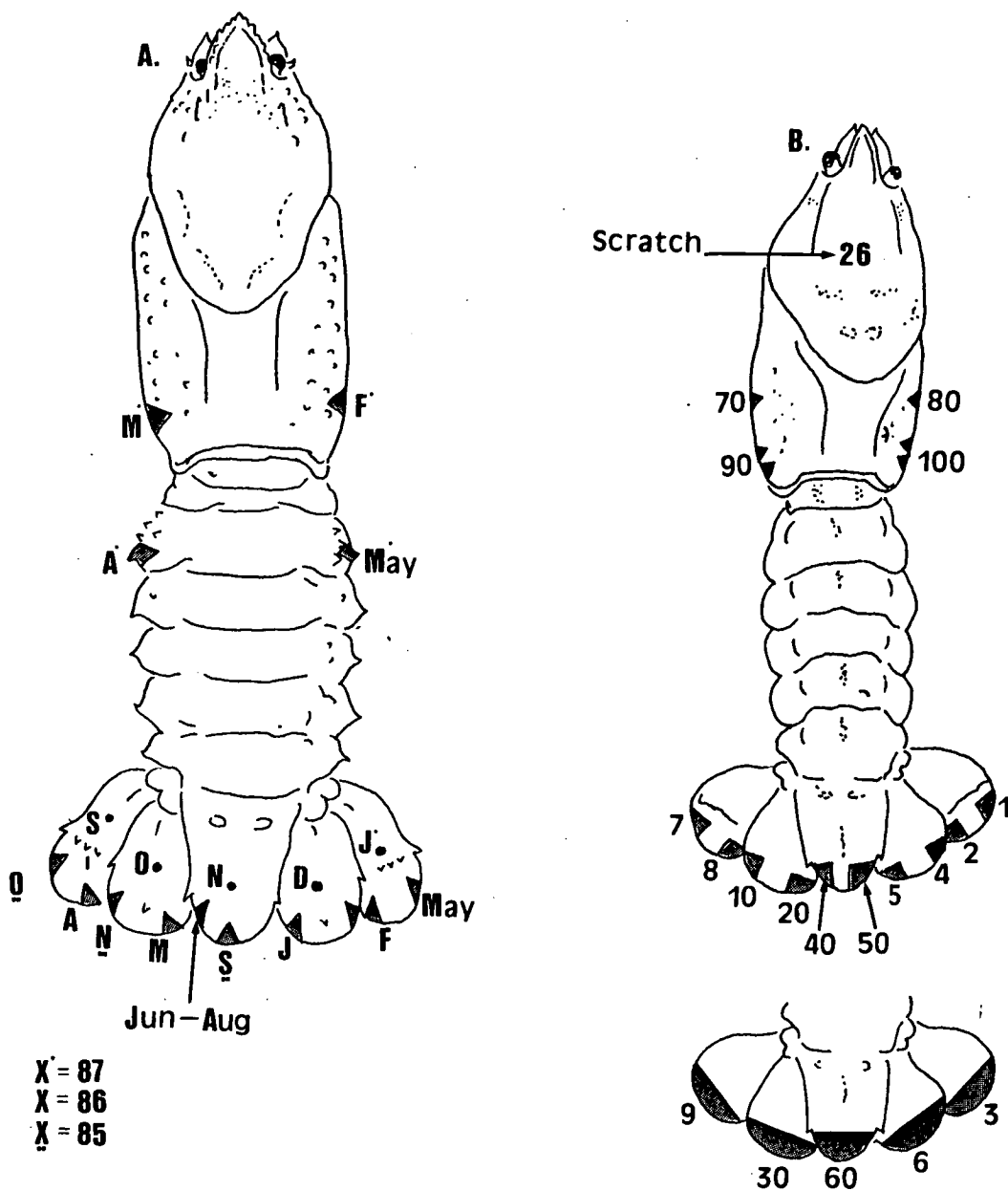


Figure 2.4 Patterns of clips and punctures on tail fan, abdomen and carapace used to mark:

A. *Astacopsis franklinii* (month of capture).

B. *Parastacoides t. tasmanicus* (individual numbers).

were marked. All but the very small juveniles (CPL < 16 mm) were marked with tail fan and carapace clips corresponding to individual numbers. The individual's number was also scratched out on the dorsal side of the carapace for quick recognition of unmolted individuals (Fig. 2.4B.). All crayfish were then released (none of the pitfall trapped animals were preserved).

2.6 Laboratory maintenance of animals

All crayfish brought back to the laboratory (at the University of Tasmania) were housed in aquaria of various sizes in ambient and constant temperature rooms with controlled photoperiod. The aquaria were filled with creek water collected at corresponding field sites. Adult *A. gouldi* were held at the Inland Fisheries Commission's field station, in large fish tanks and at the university, in a large, covered artificial pond subject to seasonal temperature and photoperiod.

Captive crayfish were supplied with a natural diet of stream leaf litter, detritus, aquatic insects and decomposing wood (*Astacopsis* species) and sections of heathland soil containing buttongrass roots (*Parastacoides* species). In addition, their diet was supplemented once weekly with fresh fish pieces and commercial fish food pellets.

CHAPTER 3. SPECIES DESCRIPTIONS

3.1 INTRODUCTION and METHODS.

The taxonomy of *Astacopsis* and *Parastacoides* has been the subject of several revisions as shown in chapter 1. With further revisions still pending (Richardson, in preparation, Horwitz, pers. comm.) it is of prime importance to clearly identify the species, subspecies and/or varieties of crayfish being dealt with in this study. Each species was therefore identified in terms of the existing taxonomy but new taxonomic and distributional information is presented.

In the diagnosis of the new forms *Astacopsis*, the morphometric descriptions and measurements were obtained from individuals preserved at various sites as a part of the broader study of population structure and reproductive biology. Individuals from numerous populations throughout each species' range were examined and compared.

Burrow descriptions were taken from field observations made at various study sites throughout the duration of the study. The burrow types were classified according to the classification proposed by Horwitz and Richardson (1986).

Some of the distributional information was obtained from Dr. A. M. M. Richardson's taxonomic collection at the University of Tasmania as well as from surveys conducted by the Inland Fisheries Commission (Tasmania).

3.2 RESULTS and DISCUSSION

3.2.1 Species descriptions: *Astacopsis*.

Two distinct forms of *Astacopsis franklinii* were recognized. These "forms" were found to differ in terms of their general morphology, reproductive biology (see Chapters 5 & 6) and distribution. As a result *Astacopsis franklinii* Gray has been divided into a "Western form" and an "Eastern form". The status of *Astacopsis gouldi* remains unaltered.

Astacopsis gouldi Clark (Fig. 3.1A).

Astacus sp. Gould, 1870, p.42.

Astacopsis franklinii Huxley 1878, p.764.

Smith 1909A, p.65; 1909B, p.109; 1912,
p.154.

Astacopsis gouldi Clark, 1936, p.35; 1939, p.119.

Riek, 1969, p.898.

Swain *et al.* 1982, p.701.

Diagnosis:

- Adults very large (largest specimen: 214 mm CPL, 4.0 kg).
- Rostrum broad, relatively shallow, V to U shaped, apex sharp terminated in single prominent spine, longitudinal carina in center of rostrum (generally well defined but can be weak on some small specimens), lateral rostral carinae raised with 3-6 blunt tubercles on each side, blunt spine at base of rostral carinae (Fig. 3.2C).
- Eyes large.
- Body armature heavy. Spines and tubercles on chelae, walking legs, carapace and abdomen. Cephalothoracic and abdominal spines much sharper in smaller specimens becoming more blunt in large specimens (Fig. 3.2C).
- Great chelae stout and very large especially in adult males (adult female chelae less robust, thinner and more elongate), outer surfaces of both fingers covered with small yellow tubercles/spines. Prominent sharp spine on merus. Held horizontally with respect to substrate.
- Sternal keel moderately sharp, with a sharp, ventrally facing spine on process between second and third pereopods.
- Male genital papilla with complete calcified tube, separated from basal portion of coxopodite in mature individuals.
- Telson calcified, without transverse suture, with single spine on lateral margins. Uropods calcified uniformly in immature individuals and adult males, decalcified distally in mature females.

Colour:

- Juveniles: basically brown with green mottling, spines and tubercles white, underside of cephalothorax ivory (see frontispiece).
- Adults: basically dark brown-green, sometimes almost black, chelae brown

Figure 3.1

A. *Astacopsis gouldi* (Inglis River).

B. *Astacopsis franklinii* Eastern form (Hobart Rivulet).

C. *Astacopsis franklinii* Western form (Clarence Lagoon).



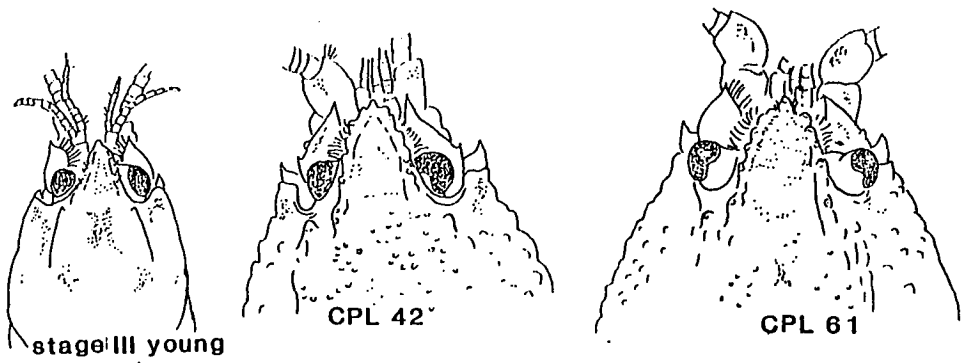
A



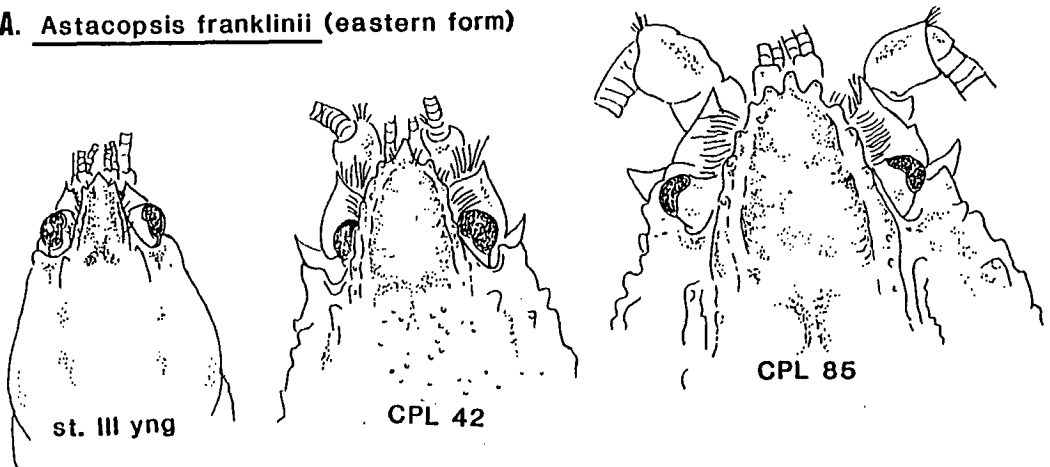
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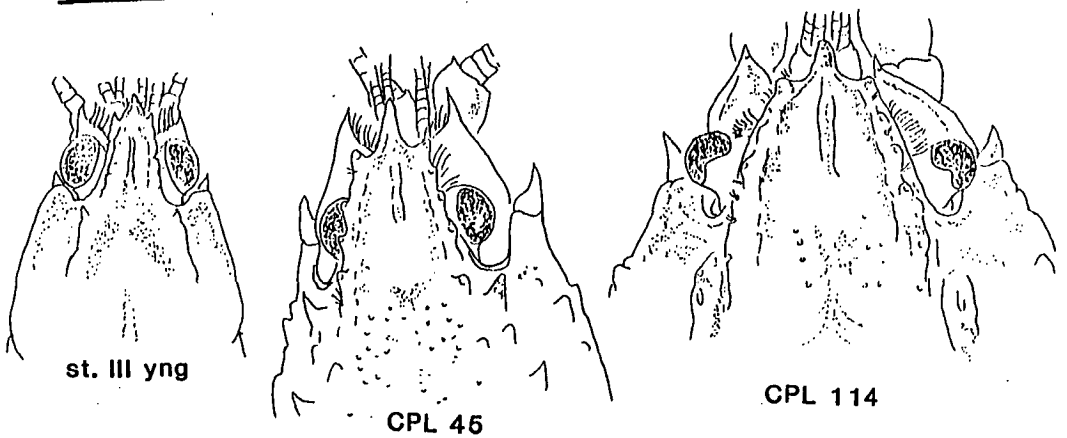
C



A. Astacopsis franklinii (eastern form)



B. A. franklinii (western form)



C. A. gouldi

Figure 3.2 Comparison of rostral morphology (stage 3 young to large adult) in *A. gouldi* and the two *A. franklinii* forms.

with greenish tips, tubercles and spines yellow. Characteristic blue marking laterally on branchiostegites and cephalic region. Blue colour morphs are often found among adults, in these the basic overall colour is bright blue (Fig. 3.1A).

Distribution:

- The known distribution of *A. gouldi* is shown in Figure 3.3 .
- New locality records: Pearly Brook (Horwitz pers.comm.); Garden of Eden Creek; Gunn's Plains Caves*; Lake Barrington; West Gawler River; Inglis River tributary (near Henrietta); Big Creek; Hellyer River; Detention River; Wilson's Creek; Sumac Rivulet.

* Specimens ranging in carapace lengths from 55 mm to 147 mm were collected from the creek running through the cave as far as 300 meters from the tourist entrance. From this study's investigations as well as the observations of Mr Des Wing, the cave's caretaker, it appears the crayfish live and breed inside the cave (Mr. Wing reports seeing berried females as well as small juveniles deep within the cave). This constitutes the first report of such a phenomenon in Tasmania.

Burrow Classification:

A. gouldi constructs type 1a and 1b burrows in streams and rivers. The burrows are usually associated with natural cover and can be detected by conspicuous semicircular mounds of excavated material (Figure 3.4).

Astacopsis franklinii Eastern form (Fig. 3.1B).

Astacus franklinii Gray, 1845, p.409.

Astacopsis tasmanicus Smith 1909A, p.65.

Astacopsis franklinii Var. *tasmanicus* Smith 1912, p.156.

Astacopsis franklinii Clark, 1936 p.34; 1939, p.119;

Riek, 1969, p.898.

Astacopsis fluviatilis Riek, 1969, p.912.

Astacopsis franklinii Swain *et al.*, 1982, p.700.

Diagnosis:

- Adults small (largest specimen: 61 mm CPL, 0.060 kg).
- Rostrum narrower anteriorly, V shaped, shallow (flat), apex terminated in single blunt spine; lateral rostral carinae blunt, with 6-7 low tubercles; small tubercle at base of carinae (Fig. 3.2A).

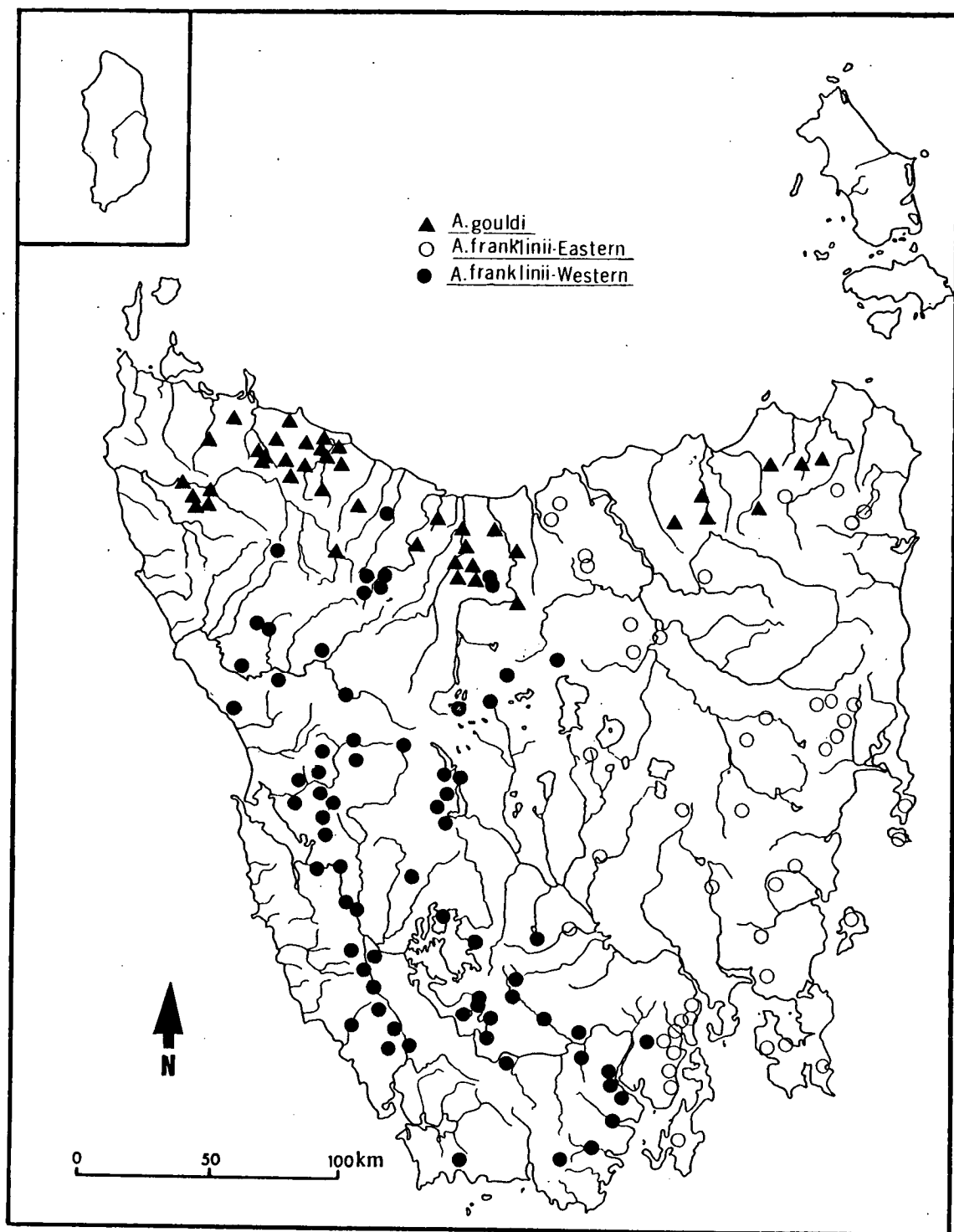
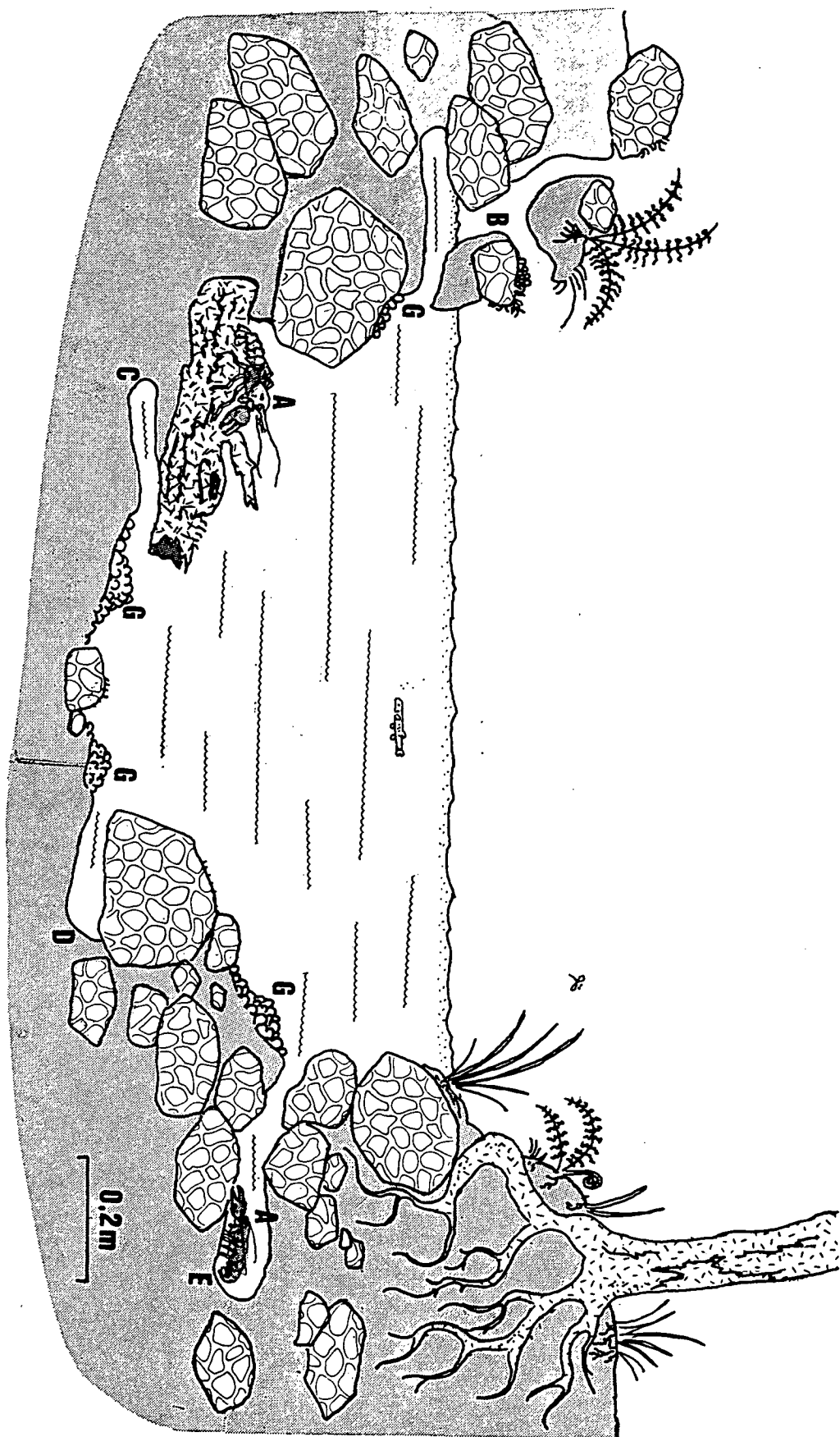


Figure 3.3 Distribution of *Astacopsis gouldi*, *Astacopsis franklinii* Eastern form and *Astacopsis franklinii* Western form. (Updated from Swain *et al.*, 1982)

Figure 3.4 Burrows of the genus *Astacopsis* (rivers and streams).

Key:

- A.** Crayfish.
- B.** Burrow in creek bank with entrances above and below water level.
- C.** Burrow under log in creek.
- D.** Burrow under rock in creek.
- E.** Burrow in creek bank with entrances below water level.
- G.** Excavated material.



- Eyes large.
- Body armature relatively heavy, spines less sharp overall, tubercles on branchiostegites small and uniform.
- Great chelae short and stout with large palm and short fingers, covered with small depressions (on palm) and tubercles (on fingers). Large spine on merus. Held horizontally with respect to substrate.
- Sternal keel blunt, lateral processes low, unsculptured, little tuberculation.
- Male genital papilla with complete calcified tube, separated from basal portion of coxopodite in mature individuals. Tube sculptured, less cylindrical.
- Telson calcified, without transverse suture, with single spine on lateral margins. Uropods calcified uniformly in immature individuals and adult males, decalcified distally in mature females.

Colour:

- Juveniles: basically light orange brown
- Adults: basically dark brown, tubercles orange, underside light orange brown (Fig. 3.1B). Blue colour morphs are infrequently found among adults.

Distribution:

- Eastern half of Tasmania, approximately east of a line from the Wellington Range in the south through the midlands to the Asbestos Range in the north (Fig. 3.3).

- New locality records: Fortescue Bay Lagoon Creek; Allen's Creek (Tasman Peninsula); Guy Fawkes Rivulet; Appledorf Creek; Tyenna River; Captain Cook Creek tributary (Bruny Island), Falls Creek tributary (Bruny Island), Browns Creek (Asbestos Range N.P.); Swan Rivulet tributary; Crocketts Creek (Schouten Island); Freycinet Peninsula: Eastern Rivulet, Jimmy Rivulet and Cooks Beach - Mt. Graham track.

Burrow Classification:

- Constructs type 1a and 1b burrows in streams and rivers (fig. 3.4). It is also known to construct type 2 burrows, well away from permanent water bodies, in at least one location on Freycinet Peninsula (Horwitz & Richardson 1986).

Astacopsis franklinii Western form (Fig. 3.1C).

Astacopsis tricornis Clark, 1936 p.36; 1939, p.120.

Astacopsis franklinii Swain *et al.*, 1982, p.700.

Diagnosis:

- Adults medium to large (largest specimen: 148.4 mm CPL, 1.00 kg).
- Rostrum broad, deep (concave), strongly U shaped, apex terminated in several spines; lateral rostral carinae sharp, raised with 5-6 raised tubercles (Fig. 3.2B)
- Eyes large.
- Body armature heavy. Spines on abdomen, chelae and walking legs, large and sharp in specimens of all sizes. Prominent raised tubercles of variable size and sharpness, laterally on branchiostegites and cephalic region.
- Great chelae large, fingers long, covered with prominent tubercles/spines. Prominent sharp spine on merus. Palm without depressions. Held horizontally with respect to substrate.
- Sternal keel sharp, lateral processes raised, sculptured, tuberculate with winglike appearance in adults.
- Male genital papilla with complete calcified tube, separated from basal portion of coxopodite in mature individuals. Tube more cylindrical, less sculptured, with prominent raised keel.
- Telson calcified, without transverse suture, with single spine on lateral margins. Uropods calcified uniformly in immature individuals and adult males, decalcified distally in mature females.

Colour:

- Juveniles: very light brown, sometimes grey; underside ivory.
- Adults basically brown to light brown; tubercles and spines yellow, those on branchiostegites especially prominent (Fig. 3.1C); blue marking on branchiostegites and cephalic region present in very large individuals; underside ivory. Blue colour morphs not noted.

Distribution:

- Western half of Tasmania, approximately from the Huon River in the south through the western edge of the Central Plateau to the Gog Range in the north (Fig. 3.3).
- New locality records: Pigsty Ponds; Pelverata Falls; Arve River tributary;

Creek draining into Reservoir Lake; Meander River; Croanna Creek; Prince Rivulet; Weld River; Harlequin Hill (burrow in buttongrass plain); Sandfly Creek (Scotts Peak road); Scotts Peak (rainforest creek draining into Lake Pedder); Giblin River; Lake Meston; Clarence Lagoon; Lake Dixon; Lake Margaret; King River tributary (near Murchison Hwy.); Murchison River; Princess River; Comstock Creek; Heazelwood River tributary; Jean Brook; Eel Hole Creek.

Burrow Classification:

- Constructs type 1a and 1b burrows in rivers and streams (Fig. 3.4). In addition, it constructs extensive burrow networks (type 1a) not associated with logs or rocks in the soft bottoms of lakes in the west of Tasmania. In one instance a juvenile individual was found in a type 2 burrow in the button grass plain near Harlequin Hill in south west Tasmania. This burrow however, appeared to have been constructed by *P. t. tasmanicus* and was in close proximity to a stream from which the *Astacopsis* may have come.

3.2.2 Key to the Genus *Astacopsis*

- 1a. Rostrum divided by a median longitudinal carina.....*A. gouldi* Clark
- 1b. Rostrum without a median longitudinal carina.....2
- 2a. Rostrum broad, concave, U shaped. Adults large with numerous, prominent spines and tubercles.....*A. franklini* Western form.
- 2b. Rostrum narrower, flat, V shaped. Adults small with less prominent spines and tubercles.....*A. franklinii* Eastern form.

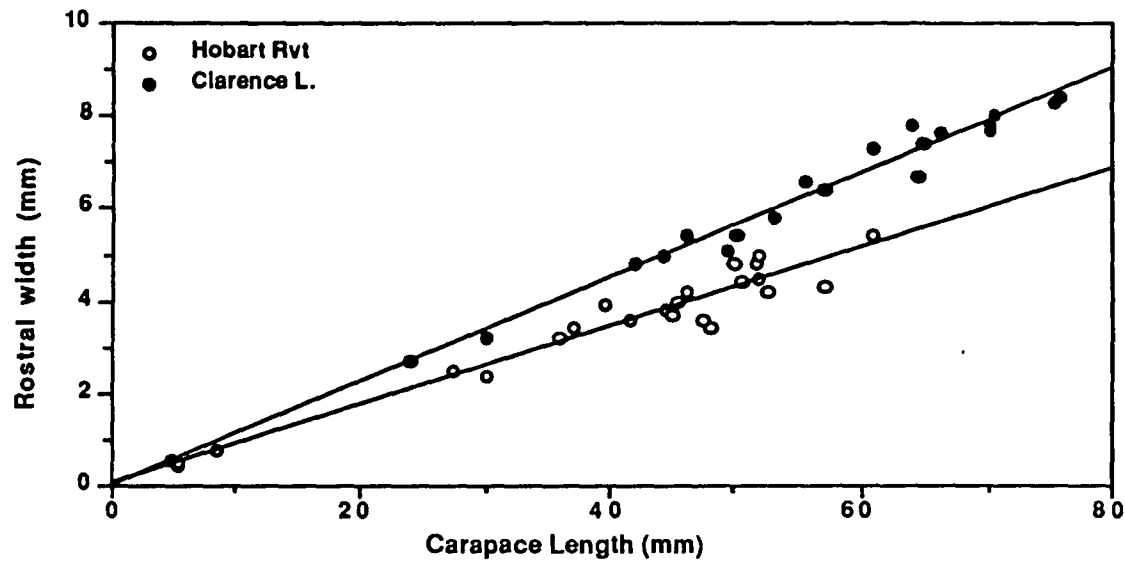
3.2.3 Analysis and discussion of taxonomic characters in the genus *Astacopsis*

The most reliable morphological characters separating the species or forms of *Astacopsis* are found on the rostrum. *A. gouldi* can be clearly distinguished from the other two species by the presence of a median rostral carina, while the two types of *A. franklinii* can be separated on the basis of rostral width and depth. Figure 3.5A & B shows the difference in the inter-ocular rostrum width between the two species

Figure 3.5

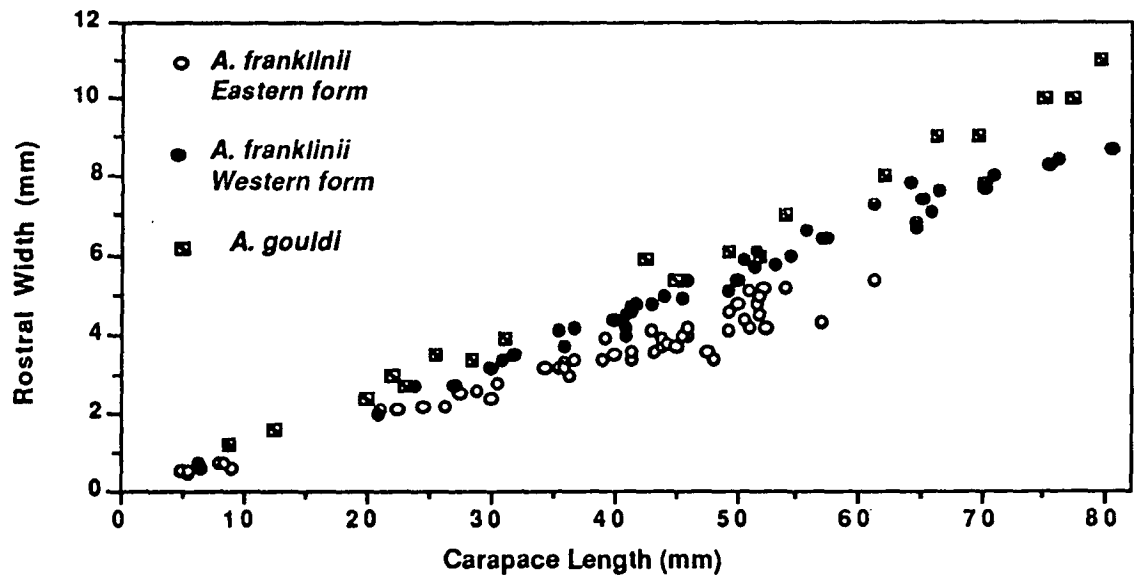
A.

The relationship between inter-ocular rostral width and carapace length in *A. franklinii* , Eastern form, from Hobart Rivulet ($y = 0.055 + 0.085x$ $r^2 = 0.953$) and *A. franklinii* , Western form, from Clarence Lagoon ($y = - 0.024 + 0.113x$ $r^2 = 0.971$).



B.

The relationship between inter-ocular rostral width and carapace length in *A. franklinii* Eastern form, *A. franklinii* Western form and *A. gouldi* (from various populations).



(The inter-ocular width was chosen as it was least affected by growth related changes in the morphology of the rostrum). In addition, the mean size adjusted inter-ocular rostral widths of the Western form (mean = 0.126, s.d. = 0.013, n = 35) and the Eastern form (mean = 0.11, s.d. = 0.006, n = 51) were found to be significantly different ($t = -7.92$, $df = 84$, $p < 0.0001$).

Although some differences in rostral morphology were noted by previous authors (Riek,1936; Swain *et al.* 1982) no characters other than the presence or absence of the median rostral carina and the morphology of spines on the lateral carinae were examined.

As shown by Swain *et al.* (1982) the exact number and location of spines are clearly an unreliable taxonomic character for separating *Astacopsis* species. There is however a clear difference in overall spininess between the two forms of *A. franklinii* especially in adult individuals. This difference was shown by Swain *et al.* (1982) who stated: "Examination of the material in our collection suggested that much of the variation in general spininess of *A. franklinii* had a geographical basis, with a reduction in spininess both from west to east and north to south". Similarly they found that " large animals were present only in collections from river systems draining north or west". This corresponds directly with the distribution of the two forms as identified in this study (Fig. 3.3). Their failure to detect the clear east west separation was probably due to sampling discrepancies (such as low numbers of crayfish from the north east region) and the large size/age range of animals in their samples.

As it is generally more difficult to recognize the specific characters in juveniles of closely related crayfish species, the best results in keying out members of the genus *Astacopsis* are therefore obtained when adults are compared.

As shown above, the two forms of *A. franklinii* are distinct in their morphology as well as their breeding biology (see Chapters 5 & 6). These differences suggest that the two "forms" can be treated at least as subspecies and may in fact constitute separate species. These findings demonstrate a further need for a careful revision of this genus. A comparison of the genus to its closest relatives *Euastacus* and *Astacoides* would also be useful.

3.2.4 Species descriptions: *Parastacoides*

As a detailed taxonomic revision is currently being prepared by Dr. A.M.M. Richardson of the University of Tasmania (see Chapter 1), no attempt was made to revise the taxonomy of this genus. The species dealt with here will therefore be referred to as forms of *P. t. tasmanicus* designated by initials (corresponding to the localities where they were studied) or presently recognized subspecies of *P. tasmanicus*.

A. *Parastacoides tasmanicus tasmanicus* (SP), (Fig. 3.6A).

Diagnosis:

- Adults small, (largest specimen: 36 mm CPL, 18.0 g).
- Carapace and abdomen poorly calcified without spines or tubercles.
- Great chelae stout, well calcified without large spine on carpus, spines and tubercles small and blunt. Held horizontally with respect to substrate.
- Tail fan well calcified, uropods rounded without spines on posterior margin.
- Colour: adults basically dark brown, sometimes greenish; juveniles light brown-grey. Underside beige.
- Mature ovarian and extruded abdominal eggs with characteristically orange brown coloured yolk (an important feature distinguishing this form from all other *Parastacoides*).

Distribution:

- Found in the Lake Pedder area of the south west of Tasmania (Fig. 3.7).

Burrow Classification:

- Constructs type 2 burrows on waterlogged sedgeland valley floors. Burrows can be quite extensive and may include several entrances as well as multiple main and feeding chambers. A detailed description of the structure of a typical burrow is shown in Figure 3.8. Burrow entrances are infrequently capped with low "chimneys" made from excavated material. Type 1b burrows are sometimes constructed in association with streams.

B. Additional forms of *P. t. tasmanicus*:

The two following forms of *P.t.tasmanicus* are also briefly dealt with in this study.

Figure 3.6

A. *Parastacoides tasmanicus tasmanicus* (SP). Harlequin Hill plain, South-West Tasmania.

B. *Parastacoides tasmanicus inermis*. Harlequin Hill (rainforest creek), South-West Tasmania.

C. *Parastacoides tasmanicus insignis*. Scotts Peak Dam area, South-West Tasmania.



A



B



C

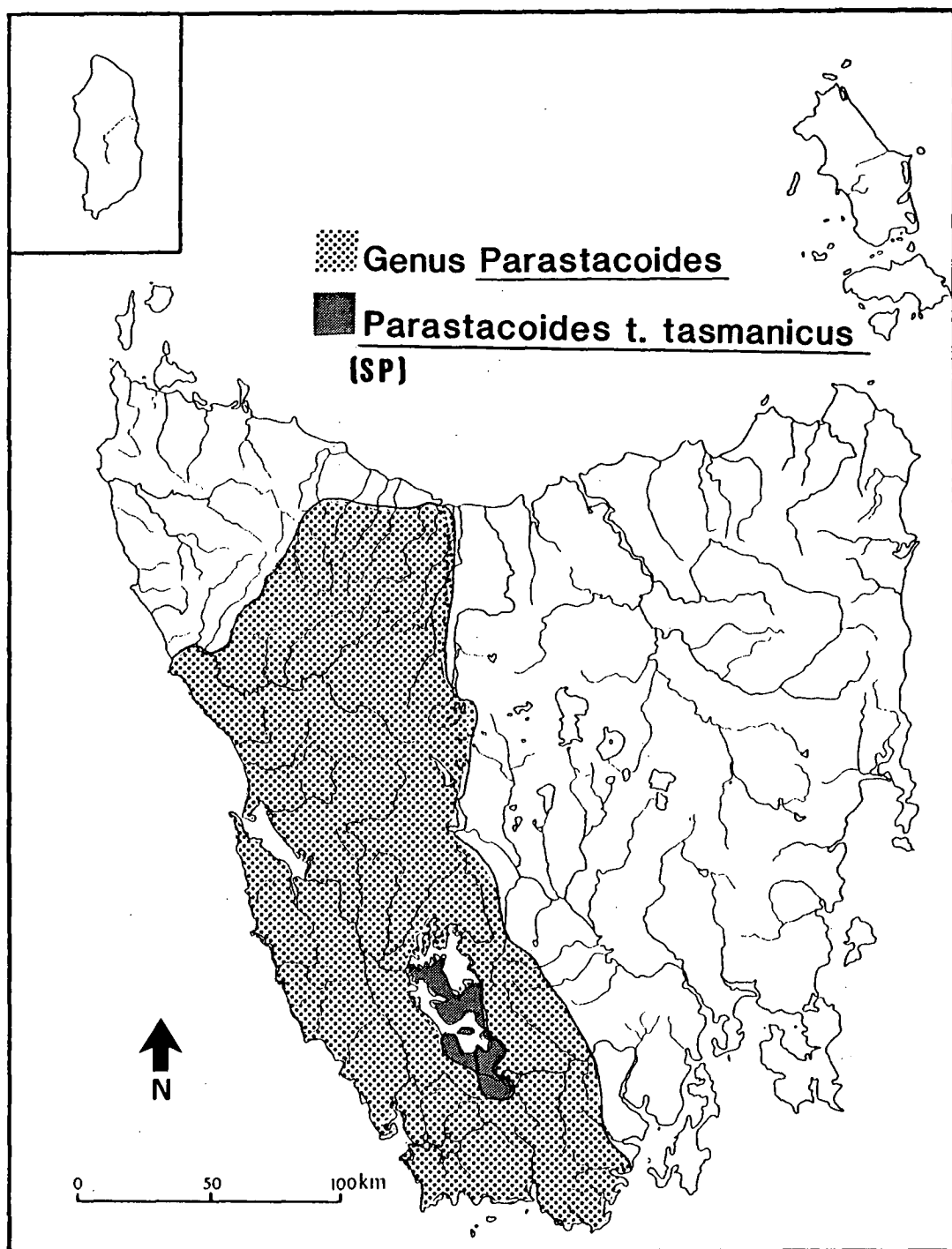
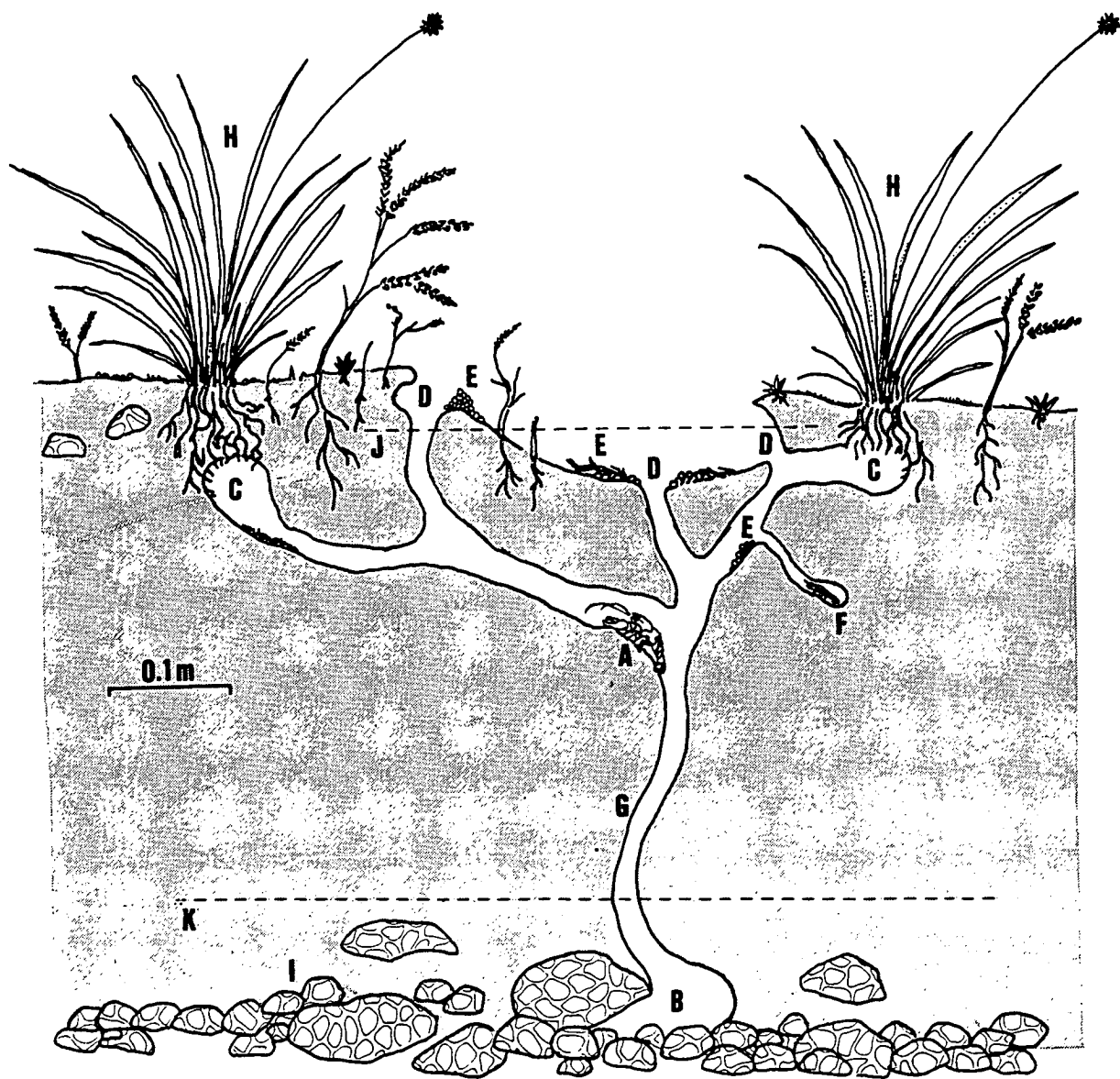


Figure 3.7 Distribution of the genus *Parastacoides*. (Courtesy of Dr. A. M. M. Richardson) Range of *P. t. tasmanicus* (SP) is inset as the shaded area around the Pedder impoundment.

Figure 3.8 Typical burrow of *P. t. tasmanicus* (SP) in the buttongrass plain at Harlequin Hill, South-West Tasmania

Key:

- A.** Crayfish.
- B.** Main chamber.
- C.** Feeding chamber with exposed buttongrass roots.
- D.** Burrow entrance.
- E.** Excavated material.
- F.** Juvenile burrow.
- G.** Downward leading tunnel.
- H.** Buttongrass tussock.
- I.** Quartzite layer.
- J.** Winter water level.
- K.** Summer water level.



1. *Parastacoides tasmanicus tasmanicus* (N)

General Diagnosis:

- Adults small, (largest specimen: 33.6 mm CPL).
- Similar to *P.t.tasmanicus* (SP) (uropods rounded, without terminal spines).

Ovarian and extruded abdominal eggs bright yellow. Occurs in the Needles Range area in south west Tasmania (see Fig. 2.1). Constructs type 2 burrows in heathland.

2. *Parastacoides tasmanicus tasmanicus* (I).

General Diagnosis:

- Adults small, (largest specimen: 29.5 mm CPL).
- Similar to *P. t. tasmanicus* (SP), (uropods rounded, without terminal spines).

Ovarian and extruded abdominal eggs bright yellow. Occurs from central west to north west Tasmania (Richardson pers. comm.). Often found in type 1a and 1b burrows in watercourses but also digs Type 2 burrows in heathland and moorland.

C. *Parastacoides tasmanicus inermis* (Fig. 3.6B).

Diagnosis:

- Adults small, overall smaller than *P.t.tasmanicus*, (largest specimen: 29 mm CPL).
- Carapace and abdomen poorly calcified without spines or tubercles.
- Great chelae stout, well calcified, setose, without large spine on carpus, spines and tubercles small and dull. Held horizontally with respect to substrate.
- Tail fan well calcified, uropods pointed with median carina produced to a single, prominent spine beyond the posterior margin.
- Colour: adults basically light to bright orange (Fig. 3.6B); juveniles light orange. Underside orange.
- Mature ovarian and extruded abdominal eggs with bright yellow coloured yolk.

Distribution:

- South west of Tasmania, South East Cape to Macquarie Harbour (Grown, 1986, Sumner, 1978).

Burrow Classification:

- Constructs type 2 burrows in heath and sedgeland. Burrows generally simpler in structure located in higher and drier areas than those of *P. t. tasmanicus*

(SP) (Richardson & Swain, 1980). Burrow entrances may be capped with short "chimneys".

D. *Parastacoides tasmanicus insignis* (Fig. 3.6C).

Diagnosis:

- Adults small, overall smaller than *P. t. tasmanicus*, (largest specimen: 28 mm CPL, 10.0 g).
- Carapace and abdomen poorly calcified without spines or tubercles.
- Great chelae stout well calcified without large spine on carpus, spines and tubercles small and dull. Held horizontally with respect to substrate.
- Tail fan well calcified, uropods pointed with median carina produced to a spine beyond the posterior margin, inner rami of uropods with additional spines on inner half of posterior margin.
- Colour: adults basically light brown with darker, symmetrical markings on abdominal somites (fig. 3.6C), juveniles light brown to orange. Underside beige.
- Mature ovarian and extruded abdominal eggs with bright yellow coloured yolk.

Distribution:

- South west corner of Tasmania: South West Cape to Lake Pedder (Growthns, 1986, Sumner, 1978).

Burrow Classification:

- Constructs type 2 burrows in heath and sedgeland habitats intermediate to those of *P. t. tasmanicus* Form 1 and *P. t. inermis* (Richardson & Swain, 1980). Burrow entrances may be capped with short "chimneys". Type 2 burrows are sometimes constructed in association with streams.

CHAPTER 4 : DESCRIPTION OF STUDY SITES

4.1 Main study sites: *Astacopsis*

4.1.1 Inglis River

The Inglis River is a medium sized river in the north west of Tasmania. Its source is located near Scolyers Hill and it empties into Bass Strait at the coastal town of Wynyard. The principal sampling area, where *A. gouldi* was studied intensively, is located in the headwaters of the river, 350 meters above sea level, south west of the village of Henrietta (Fig. 2.1). Access to the site was gained by the Choveaux forestry road. The 750 meter stretch of river sampled flows in part through a Forestry Commission pine plantation, and in part through privately owned native forest. The river in this portion consists of relatively shallow (0.2 m - 1m) sections in between deeper pools (1 - 2.5 m). The gradient of the watercourse was very steep in some portions and the sampling area thus contained numerous rapids and waterfalls. The bottom consisted of gravel and sand with rocks, boulders and submerged trunks of native trees. Detritus and leaf litter was abundant in slower flowing portions. Several large logjams were present in the sampling area.

The river flowed mostly through native forest in the sampling area and was therefore relatively well shaded by the canopy of the streamside vegetation which included large Eucalypts (mostly *Eucalyptus obliqua*), Blackwoods and Wattles (*Acacia* sp.), Tea Tree (*Leptospermum* sp.), Dogwood (*Pomaderris apetala*), Tree ferns (*Dicksonia antarctica*) and various ferns .

The annual rainfall in the region is high (approximately 1200 mm), with the highest rainfalls occurring from autumn to spring (Figure 4.1). Water levels and flow rates reflected the rainfall patterns varying from high and very fast in spring and autumn, to slow and very low in mid-Summer (Fig. 4.3). During periods of very heavy rain the water level and flow rose very rapidly (up to 0.5 m in 10 hours) creating deep pools and long sections of white water rapids. The flow of the river is not subject to any manmade regulation. Hughes (1988), in her hydrological classification of Tasmanian rivers found they could be divided into four groups. Group 2 in the dry south-east of the state, exhibited regimes similar to the drier

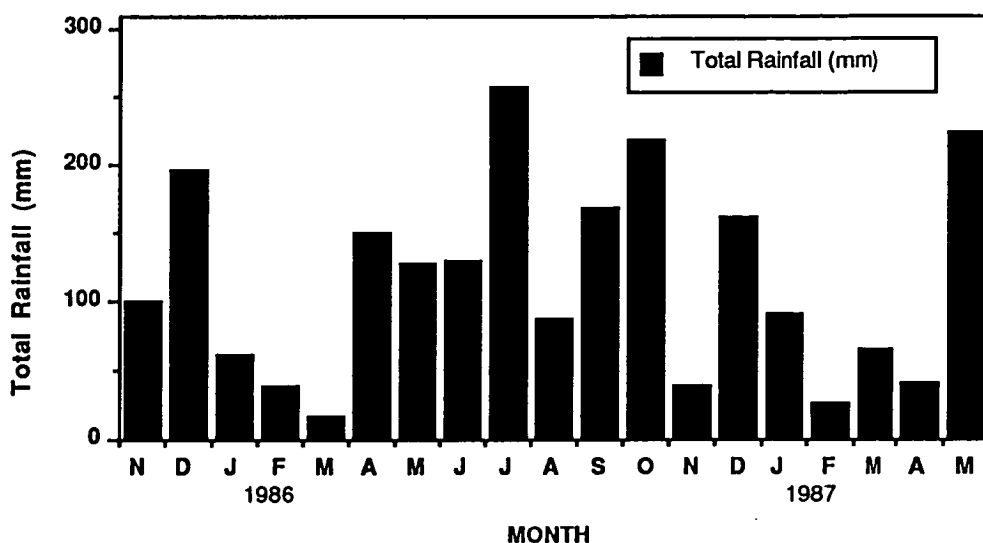


Figure 4.1 Total monthly rainfall at Yolla, Tasmania (14 km north of Inglis River sampling site).

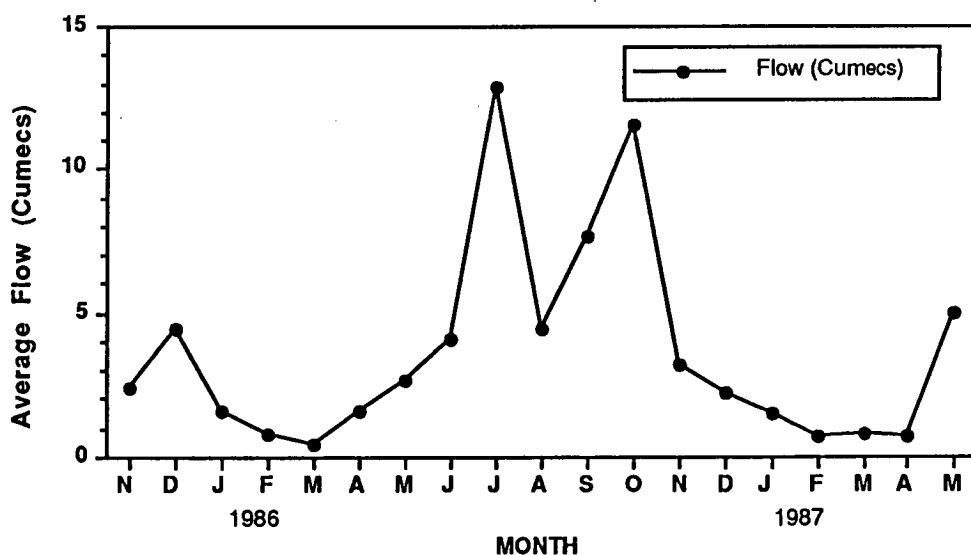


Figure 4.2. Average monthly flows in the Inglis River measured at the Inglis - Flowerdale junction.

Figure 4.3 Flow and water levels in the Inglis River:

A. Spring (October)

B. Mid-summer (February)



A



B

Australian mainland areas, group 3 in the wettest western region had no analogue in mainland Australia, while groups 1 and 4 had more temperate regimes. She included the Inglis River in group 4 which was characterized by having the most normal distribution of annual flows and by having mean annual runoffs as well as overall flow regimes similar to rivers in temperate regions. A summary of the monthly flows in the Inglis River (taken downstream, at the Inglis-Flowerdale junction) for the duration of this study is shown in Figure 4.2.

Water temperatures in the sampling area remained relatively cool throughout the year (Fig. 4.4) with a mean yearly temperature of 10.0 °C (s.d. = 4.0). The lowest temperature recorded was 5.2 °C (Aug.) while the highest was 18.0 °C (Feb.-Mar.). Air temperatures of the region, although somewhat warmer, reflected the general pattern of water temperatures (Fig. 4.5). The highest air temperature measured was 25°C (Feb.-Mar.) while the lowest was -1.0 °C (Jun.-Jul.).

The pH measurements for 1985-87, taken by the Rivers and Water Supply Commission at the Inglis-Flowerdale junction station ranged between 5.6 and 7.5 (mean = 6.2, st.dev. = 0.5, n = 13).

Crayfishes present in the sampling area included *Astacopsis gouldi*, *Parastacoides tasmanicus tasmanicus* Form 3, and *Engaeus fossor*.

4.1.2 Hobart and Guy Fawkes Rivulets

Hobart Rivulet and Guy Fawkes Rivulet are two small, parallel streams draining the eastern face of Mount Wellington. Hobart Rivulet has its source near The Springs, 600 meters above sea level, descends the mountain relatively undisturbed for 4 kilometers then enters Hobart suburbs near the Cascade Brewery, continues for an additional 3 kilometers before finally flowing into the Derwent River in central Hobart where its course has been severely modified. The source of Guy Fawkes Rivulet is also located at the 600 meter level but it is one kilometer north of the origin of Hobart Rivulet. The stream descends relatively undisturbed down Mount Wellington for 2.7 kilometers before flowing into Hobart Rivulet at the Cascade Brewery.

The two principal sampling areas where *A. franklinii* Eastern form was studied intensively were the following: in Hobart Rivulet, a 500 meter stretch of the stream parallel to the Rivulet Track enclosed between two bends of Strickland Avenue; in Guy Fawkes Rivulet a 1 kilometer stretch of the stream above the Cascade Brewery

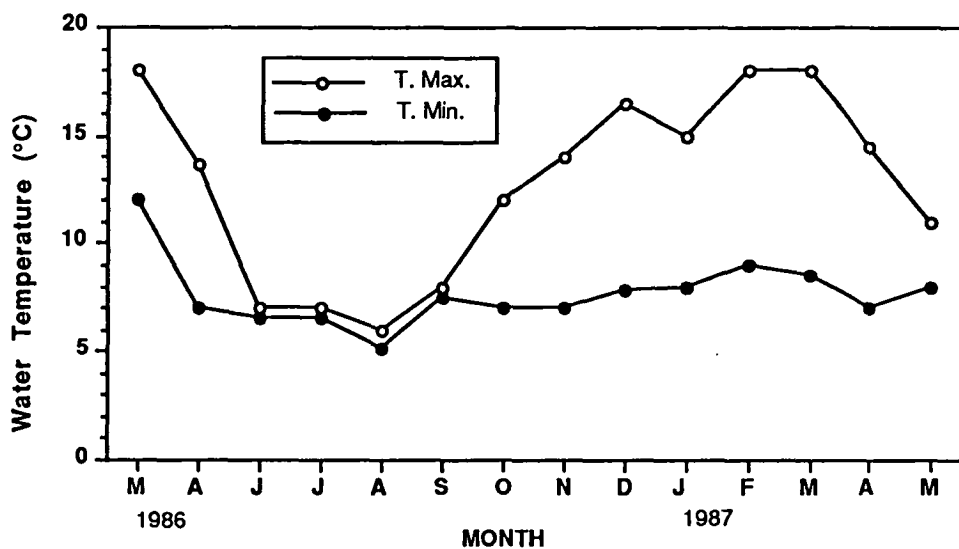


Figure 4.4 Maximum and minimum water temperatures at the Inglis River sampling area.

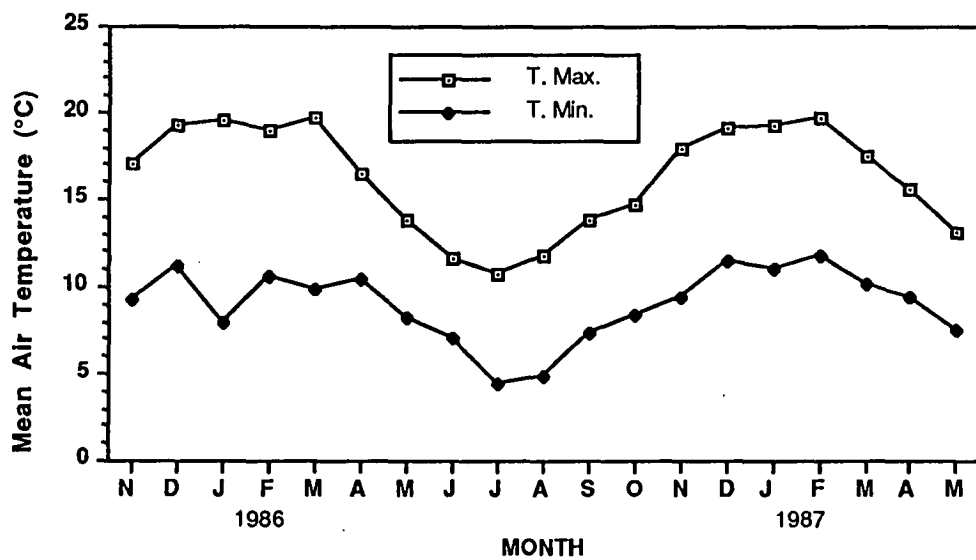


Figure 4.5 Mean air temperatures at the Elliot Research Station (17 Km north of the sampling area).

and parallel to Old Farm Road. The two areas were located near the junction of the two streams, approximately 1 kilometer apart, at 200 to 300 meters above sea level. Both sampling areas were very similar. The two streams were generally shallow (0.10 - 0.50 m) with a few deeper pools (1.0 - 1.6 m). Their bottoms consisted of sand, gravel, boulders and some submerged tree limbs and trunks. Leaf litter and detritus were abundant. The streams flowed for the most part through native forest and were therefore well shaded by its canopy. The streamside vegetation which consisted of wet sclerophyll forest and permanently wet gully communities with thick undergrowth (Radkowsky & Radkowsky, 1977) included Wattles (*Acacia dealbata*, *A. verniciflua*, *A. novae-zealandiae*.), Stringybarks (*Eucalyptus obliqua*), Tea Tree (*Leptospermum scoparium*), Dogwood (*Pomaderris apetala*), Lacewood (*Phebalium squamentum*) and various ferns (*Polystichum proliferum*, *Blechnum procerum*, *B. fluviatile*).

As the two streams sampled were in close proximity and with similar physical features and vegetative cover, their flow and temperature regimes were almost identical and were therefore grouped in the subsequent climate analysis.

The annual rainfall for the city of Hobart is approximately 650 mm, but higher rainfalls occur closer to the summit of Mt. Wellington (annual rainfall = 1200 mm). As shown in Figure 4.6 the rainfall in the Hobart region varies less seasonally but the summer months tend to be generally drier. Note: in the period of Dec. 85 - Jan. 86, unusually high (record) rainfall levels occurred. Water levels and flow in the sampling areas rates reflected the rainfall patterns with low to very low flows and levels in the drier mid-summer months (Feb.- Mar.) and high to very high flows in the wetter months (May, Oct- Dec.).

Water temperatures in the sampling areas were relatively cool throughout the year (Fig. 4.8) with a mean yearly temperature of 8.8 °C (s.d. = 3.9). Snowfalls which may occur at the summit of Mt. Wellington, during all months of the year (Fig 4.7), cause cool "flushes" within the streams following the usually rapid snow melt. This is reflected by the relatively large differences in the maximum and minimum temperatures during the warmer months. The lowest temperature recorded was 3.0 °C (Jul.) while the highest was 17.0 °C (Nov.). Air temperatures of the Hobart region, although somewhat warmer, reflected the general pattern of water temperatures (Fig. 4.9). The highest air temperature ranged from 25 to 35 °C (Summer) while the lowest were between -1 and 6 °C (Winter).

The pH measurements for 1985-87, taken by the Rivers and Water Supply

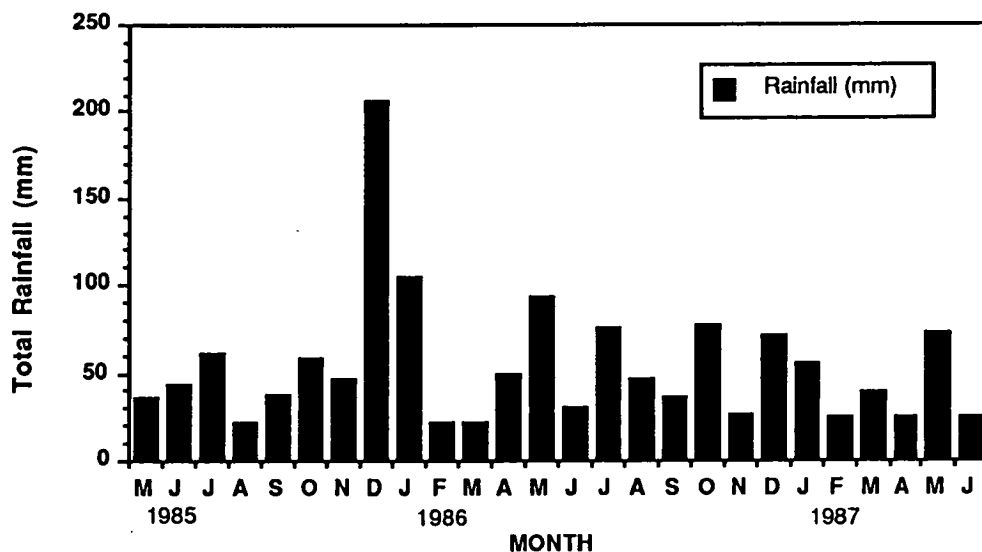


Figure 4.6 Total monthly rainfall for the town of Hobart from May 1985 to June 1987.

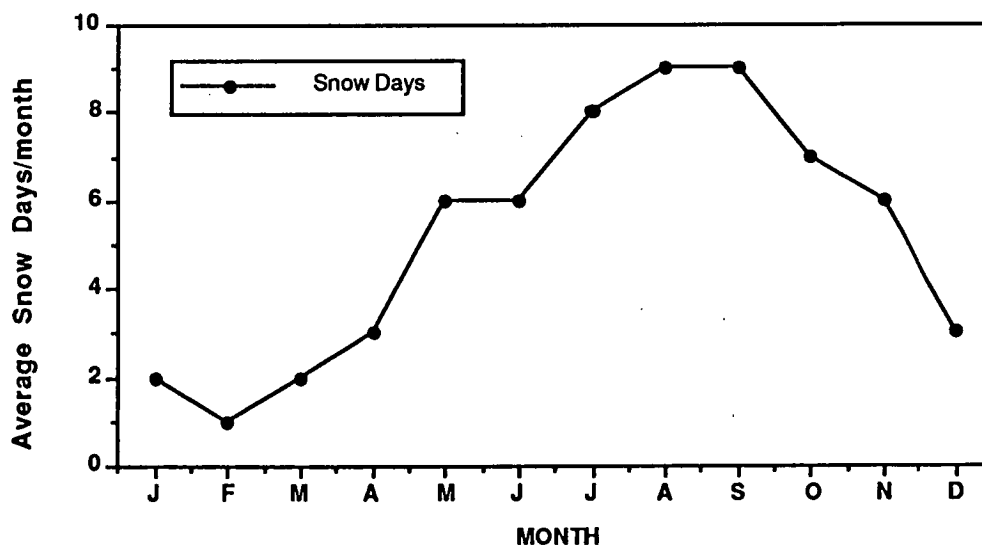


Figure 4.7 Average number of days per month when snow has been observed on Mt. Wellington.

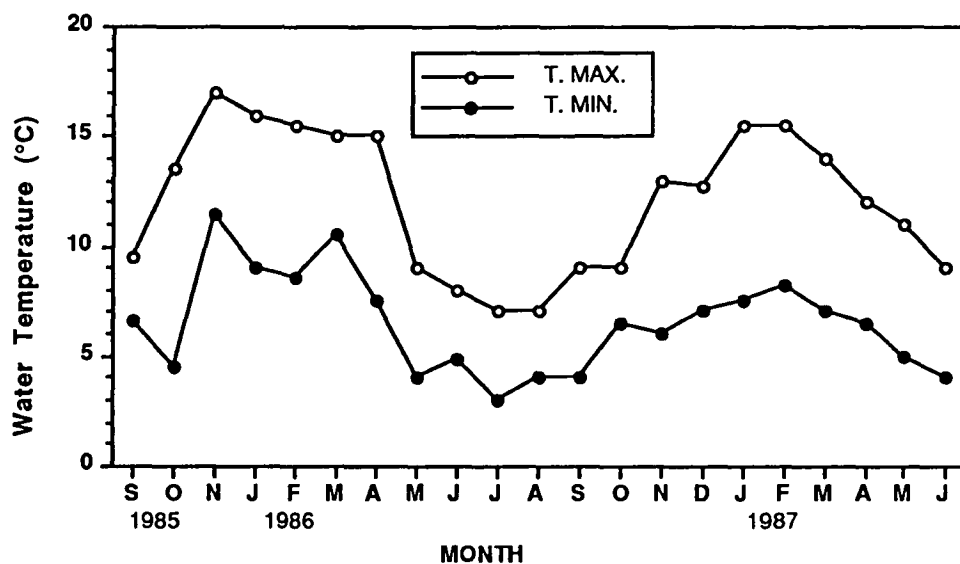


Figure 4.8 Maximum and minimum water temperatures in Hobart and Guy Fawkes rivulets (combined data).

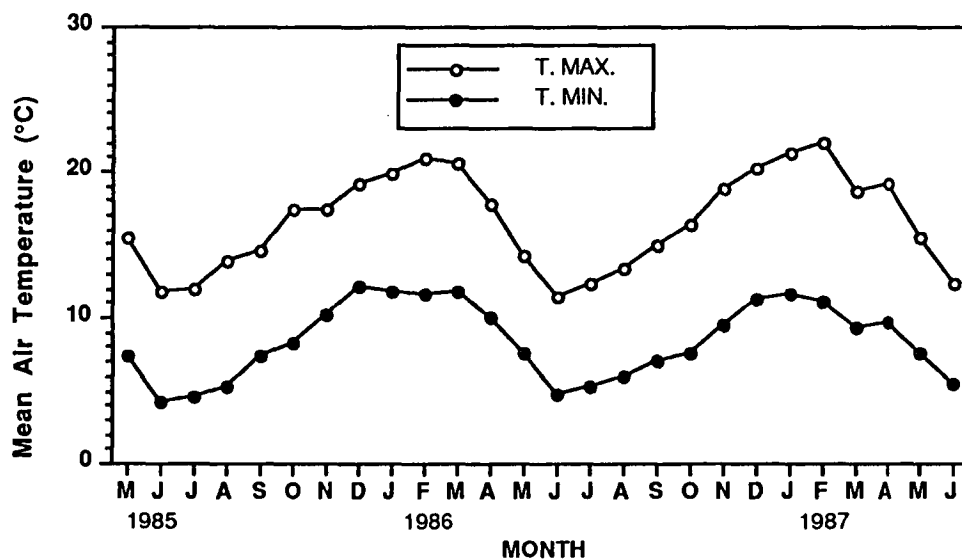


Figure 4.9 Mean monthly air temperatures for the town of Hobart (May 1985 - June 1987).

Commission in water courses draining Mt. Wellington ranged between 5.1 and 8.1 (mean = 6.6, st.dev. = 0.5, n = 13).

A. franklinii is the only freshwater crayfish species present in both rivulets.

4.2 Main study site: *Parastacoides*

4.2.1 Harlequin Hill Plain

The Harlequin Hill Plain is located between the Anne Range and the new Lake Pedder in the South West National Park in south western Tasmania. The sampling area where *P. t. tasmanicus* (SP) and *P. t. inermis* were studied is located between Harlequin Hill (on the shore of Lake Pedder) and Scotts Peak Road road, 300 meters above sea level (Fig.4.10). It is bordered by Twin Creeks in the south and by Condominium Creek in the north. The area slopes from higher, drier ground near the road to a swamp near the lake shore. The plain contained some drier ridges and several very small streams.

The soil in the area can be characterized has been as a podzol- peat and its properties have been described in detail by Bowman *et al.*(1986). The vegetation in the study area can be characterized as Blanket Moor: Pure Buttongrass (Jarman *et al.*,1988) and is dominated by Buttongrass tussocks (*Gymnoschoenus sphaerocephalus*). Other plants in this sedgeland included *Leptospermum scoparium*, *Bauera rubioides*, *Sprengelia incarnata*, *Epacris lanuginosa.*, *Drosera binata* and *Lycopodium laterale*. The plant communities of the area have been described in detail by Jarman *et al.* (1988) and Lake and Newcombe (1975).

The annual rainfall in the region is very high (approximately 2500 mm). For the duration of the study, heavy rainfalls occurred throughout the year (Figure 4.11). Long term records show however that January, February and March tend to be somewhat drier. The water levels in the crayfish burrows fluctuated according to the rainfall so that during the wet months the burrows were completely full, with large surface pools while during the dry months only a little water remained in the bottom chambers.

Water temperatures in the crayfish burrows (taken 30 cm below the soil surface) were cool for most of the year but the maxima reached relatively high temperatures in the summer months (Fig. 4.12). The mean yearly temperature was 10.8 °C (s.d. =



Figure 4.10 The Harlequin Hill sampling area. View from Harlequin Hill on the shore of Lake Pedder.
The Anne Range is in the background.

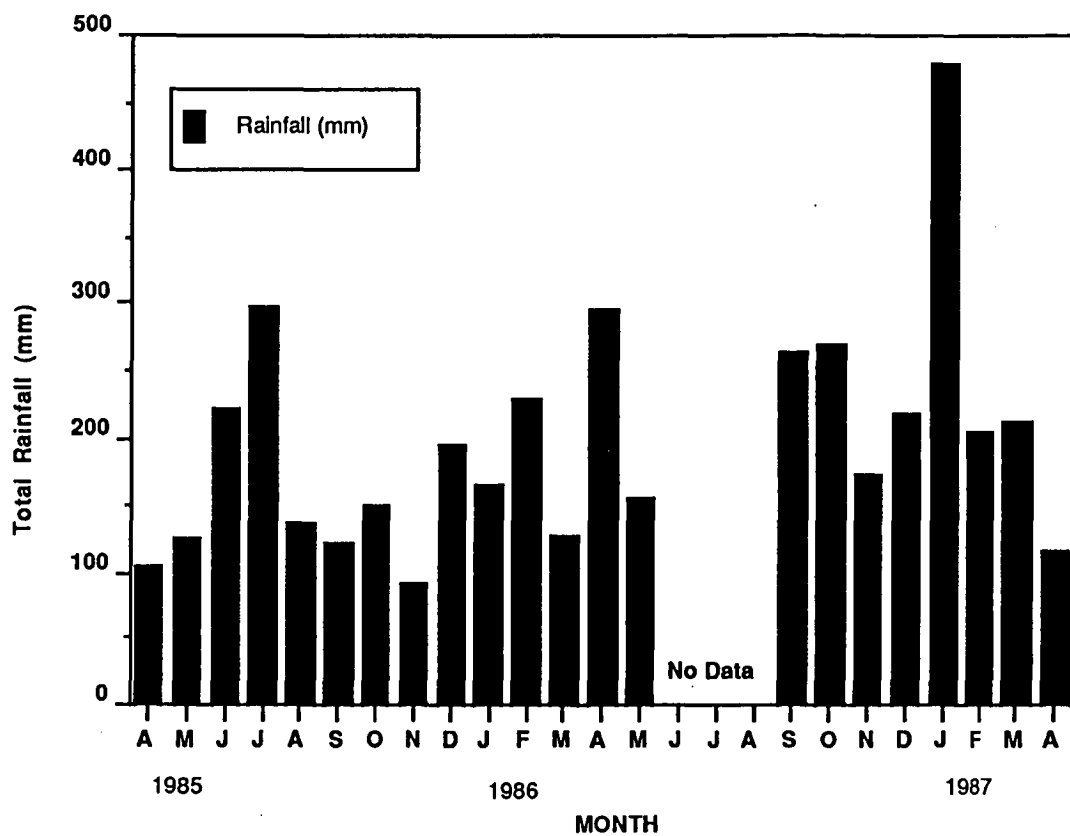


Figure 4.11 Total monthly rainfall at Strathgordon (25 km north west of the Harlequin Hill sampling area).

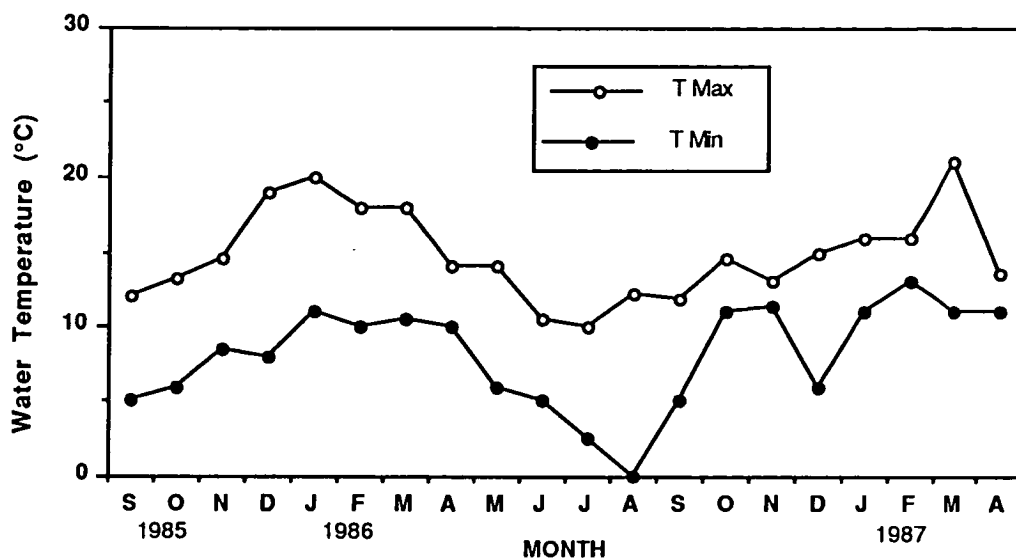


Figure 4.12 Maximum and minimum burrow water temperatures (30 cm below ground level) at the Harlequin Hill sampling area.

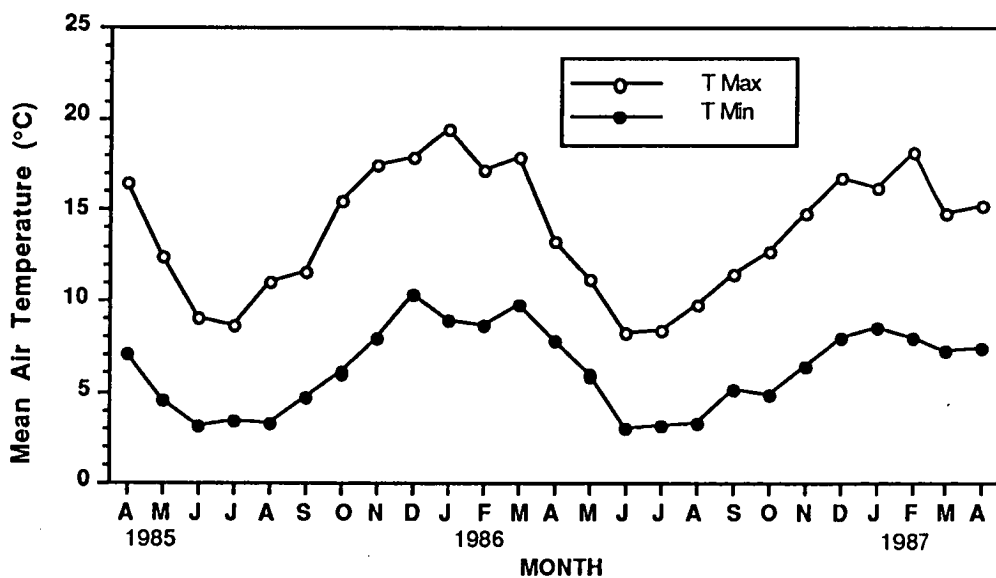


Figure 4.13 Mean monthly air temperature at Strathgordon (25 km north west from the Harlequin Hill sampling area).

4.8). The highest temperature recorded was 20.0 °C (Jan.) while the lowest was 0 °C (Aug.). During cold winter nights ice formed on the surface pools of the burrow openings. Air temperatures although warmer, reflected the general pattern of water temperatures (Fig. 4.13). The highest air temperatures approached 30 °C while the lowest were just below the freezing point.

The burrow water is tanned brown and ranges in pH from 3.7 to 5.6 (Swain et.al. 1987). Lake and Newcombe (1975) describe in detail the water chemistry of burrow water at a nearby, comparable site.

P. t. tasmanicus (SP) and *P. t. inermis* were the two crayfish species found in the sampling area.

CHAPTER 5: REPRODUCTIVE MORPHOLOGY AND ANATOMY

5.1 INTRODUCTION

In all members of the infraorder Astacidea (freshwater crayfishes and clawed marine lobsters) the female genital apertures (gonopores) are located on the coxae of the third pereopods while the male apertures are located on the coxae of the fifth pereopods. The gonopores are the external openings of the oviducts or vasa deferentia through which ova or sperm are extruded.

Clawed lobsters and crayfishes of the northern hemisphere possess specialized copulatory structures in both sexes. In the Nephropidae, Astacidae and Cambaridae males have modified first and second abdominal pleopods for sperm transfer. During copulation, the first pair is inserted into the females' sperm receptacle or leaned up against the sternum, forming a tube through which sperm passes from the male gonopores to the female receptacle or onto the sternal plates in the form of a spermatophore. The second pair act to support the first pair and can also aid in the transport of the sperm.

In the Cambaridae the first pair of pleopods undergoes cyclic dimorphism (Faxon, 1884; Croker & Barr, 1968; Hobbs, 1981; Hamr & Berrill, 1985), alternating between a reproductive form or Form 1 and a non-reproductive form or Form 2. Form 1 is attained for the first time when young males molt to maturity, their copulatory stylets (first pair of pleopods) becoming strong with heavily sclerotized and sharply pointed projections. Form 2 is found in immature individuals and in mature males between periods of sexual activity. Mature males molt into Form 1 prior to each mating season, as copulation can only occur between Form 1 males and mature females. Such cycling in stylet morphology does not occur in the male Astacidae, where the stylets remain in one constant form.

Female Nephropidae and North American Cambaridae possess a specialized receptacle for sperm (seminal receptacle or annulus ventralis) on the sternum between the coxa of the fourth and fifth pereopods. The receptacle contains a short blind canal in which sperm is stored after copulation until the female is ready to extrude her eggs. Females of the Astacidae and of the Asiatic Cambaridae (*Cambaroides* sp.) do not have a seminal receptacle but the sternum appears to be somewhat modified for sperm adhesion in at least some members of these families (Thomas, 1987).

In his review of the methods of sperm transfer and storage in the Decapoda, Bauer (1986) proposed that the degree of complexity of male gonopods and female sperm storage organs exhibited by a taxon is a measure of phylogenetic distance from the ancestral state. The morphology of the male and female genital apparatus has been used as one of the main taxonomic characters in the classification of the Cambaridae and the Astacidae (Hobbs, 1974 & 1988). The most advanced groups in the above classification are generally those with the most complex male and female genitalia.

The Parastacidae (southern hemisphere crayfishes) do not appear to possess any specialized copulatory structures. They lack the first abdominal pleopods in both sexes and females do not have a seminal receptacle. The second pleopod is unmodified in males but the external openings of the vasa deferentia (gonopores) terminate in conspicuous papillae. Riek (1972) noted that these papillae were not uniform throughout the Parastacidae and he used their form as a taxonomic character in his review of the family. Shipway (1951) and Turvey (1980) noted that the papillae become more erect and inflated in reproducing males. Female gonopores although also superficially simple, have been shown to undergo changes, such as decalcification, increased setation and swelling with the attainment of maturity in at least some parastacids (Turvey, 1980; Horwitz, 1988). Intersex individuals, having both male and female gonopores, are commonly found in some parastacid genera such as *Cherax* (Woodland, 1967; Johnson, 1979; Lake and Sokol, 1986), *Engaewa* and *Engaeus* (Horwitz, 1986 & 1988), but the significance of this phenomenon has not been investigated. Sperm transfer appears simple, as during copulation males deposit a spermatophoric mass onto the lower sternum of females (Lake & Sokol, 1986; Sammy, 1988). Bauer (1986) expresses the view that the loss of the first pleopods and any reproductive structure on the second pleopod of male Parastacidae represents a reduction from the ancestral condition.

It is interesting to note that the Palinuridae or spiny lobsters also apparently lack any specialized copulatory structures, with the first pleopods of both sexes and the female seminal receptacle being absent (Paterson, 1968; Aiken & Waddy, 1980).

The anatomy of the reproductive system of lobsters (Nephropidae and Palinuridae) and northern hemisphere crayfishes (Astacidae and Cambaridae) has been described in some detail (Huxley, 1880; Word & Hobbs, 1958; Lowe, 1961; Farmer, 1974; Aiken & Waddy, 1980; Arrignon, 1981; Dudenhausen & Talbot, 1983) but the literature contains very little information on the anatomy and

development of the parastacid gonad. Except for two unpublished accounts (Johnson, 1979; Turvey, 1980) only Morrissy's partial description of the ovary of *Cherax tenuimanus* is available (1970).

Sexual dimorphism (presence of secondary sexual characteristics) in mature Nephropidae, Astacidae and Cambaridae has also been well documented (Yonge, 1937; Stephens, 1952; Weagle & Ozburn, 1970; Farmer, 1974b; Stein, 1976; Phillips *et.al.*, 1980; Linquist & Lahti, 1983; Thomas, 1983; Price & Payne, 1984; Hamr & Berrill, 1985; Thomas & Ingle, 1987). In males, these characteristics include larger chelae, functional changes in first and second abdominal pleopods, and the presence of "copulatory" hooks on the ischia of third to fourth pereopods. In females sexual dimorphism is demonstrated by the presence of a seminal receptacle, wider and deeper abdominal pleura, the presence of glair glands (also known as "cement glands") in uropods and/or pleopods, increased abundance of abdominal setae and the occurrence of oostetae on pleopods.

The Parastacidae do not show the conspicuous sexual dimorphism in pleopod morphology but males of *Cherax destructor* attain larger size overall and have larger chelae while females have broader abdomens and develop filamentous oostetae on pleopods (Johnson, 1979; Sokol, 1988). Males of the tropical species *Cherax quadricarinatus* have prominent membranous red patches on their chelae (Sammy, 1988). Members of the genus *Astacoides* apparently do not have dimorphic chelae but the abdomens of females are broader than those of males (Hobbs, 1987). Oostetae have also been noted on females of *Euastacus spinifer* (Turvey, 1980), *Cherax tenuimanus* (Morrissy, 1970) and *Paranephrops planifrons* (Hopkins, 1967). A report of glair glands on females of a species of *Cherax* (Mills, 1983) remains unsubstantiated. Reproductive females of *Engaeus tuberculatus* and *E. hemicirratulus* were shown to exhibit numerous secondary sexual characteristics such as a flap on the second abdominal segment, decalcification of abdominal pleura and uropods as well as increased proportions of abdominal pleura, pleopods and uropods (Horwitz, 1988). These secondary sexual characteristics (the flap in particular) apparently occur on all but one of the species of *Engaeus* as well as berried females of the genera *Engaeawa*, *Geocharax*, *Gramastacus* and *Tenuibranchiurus* (Horwitz, 1986 & 1988).

This chapter examines the reproductive anatomy and morphology of the crayfishes in the Tasmanian genera *Astacopsis* and *Parastacoides*. The morphology

of various body parts as well as the development of male and female gonads and gonopores is examined in detail from the postlarva to large adult. Sexual dimorphism is documented. The descriptions presented here are the first of their kind, not only for the two genera studied but, in many cases, for the Parastacidae in general. Changes in body proportions, gonopores and gonads are used to estimate the size of maturity and breeding condition of the crayfishes examined. The two genera are compared to each other as well as to other members of the Parastacidae. The differences and similarities of parastacid, astacid, cambarid and nephropid reproductive systems are discussed in terms of their evolutionary significance.

5.2 METHODS

The morphology of genitalia as well as the sexual dimorphism of body parts and appendages in males and females were described from examination and measurement of specimens collected and preserved during monthly sampling. Measurements taken in the field and in the laboratory are illustrated in Figure 5.1. In the case of *A. gouldi*, as the number of large adults caught in this study was relatively low, some measurements used in the morphometric analysis were obtained from a collection of large adults from various locations, lodged with The Inland Fisheries Commission, Tasmania.

Glair glands and the anatomy and development of gonads were described from crayfishes collected and preserved during the mating season (March for *Parastacoides*; May for *Astacopsis*).

Crayfishes of a range of sizes and ages were examined in order to document the development of the reproductive morphology/anatomy throughout each species' life cycle.

All illustrations were made under a binocular dissecting microscope with the aid of a camera lucida.

Carapace length (CPL) was used as the standard measure of size for the crayfish examined. Weight measurements were taken as wet weights of preserved animals for all species except for *A. gouldi* where weights of live animals were used. Preserved animals were dried off with a paper towel and then weighed on a toploading electronic balance. Live animals were weighed in the field with a spring

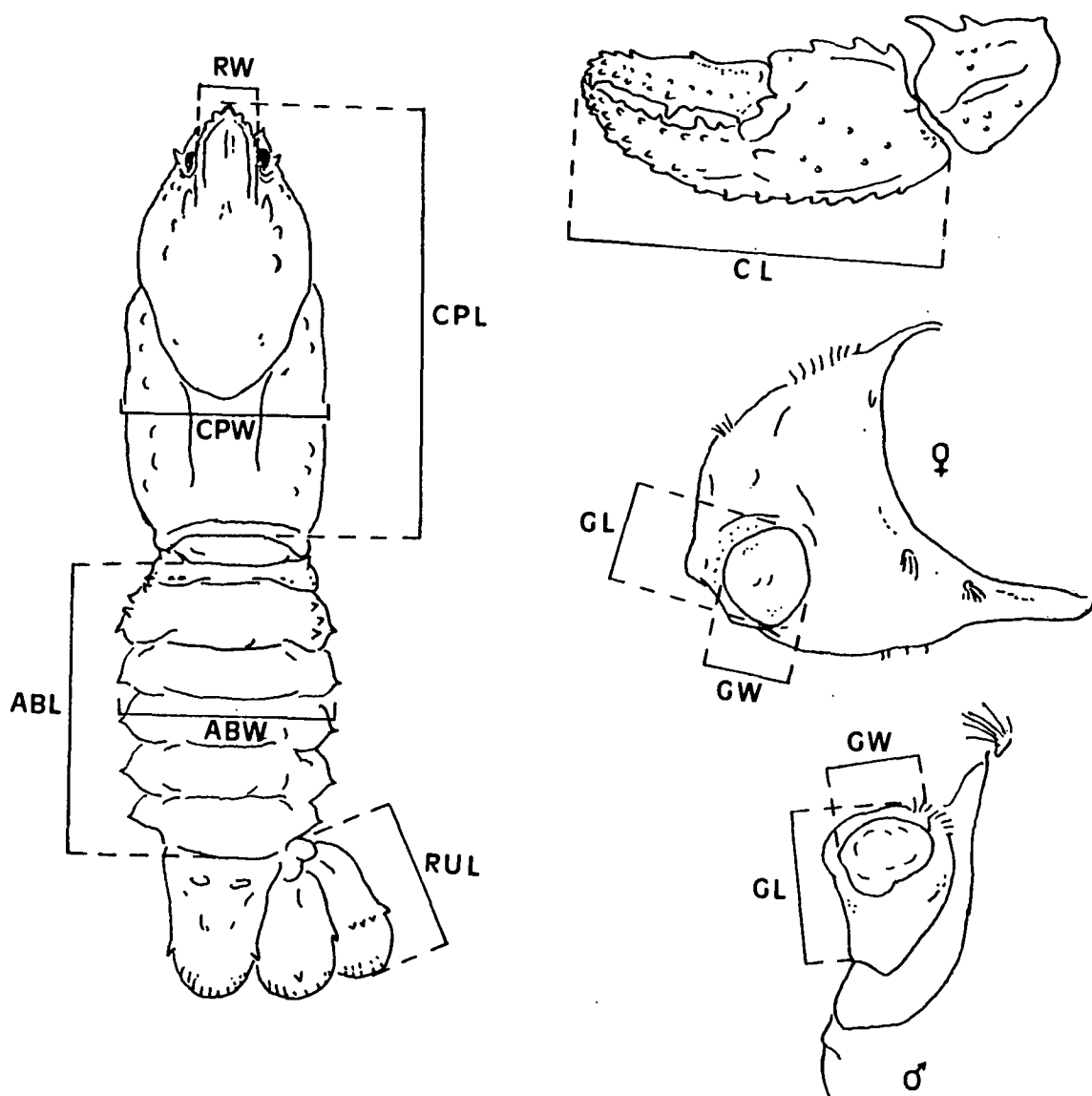


Figure 5.1 Morphological measurements taken in the field and laboratory. CPL: carapace length; CPW: carapace width; ABL: abdomen length; RUL: right uropod length; RW: rostral width; CL: cheliped length (CLR: right cheliped, CLL: left cheliped); GL: gonopore length; GW: gonopore width.

loaded portable balance.

5.3 RESULTS

5.3.1. Anatomy and development of gonads

A. The female gonad:

The ovary of *Astacopsis* and *Parastacoides* is located posterior to the stomach, resting on top of the hepatopancreas directly below the heart (Figures 5.2 & 5.3). The ovaries of both *Astacopsis* and *Parastacoides* consist of two elongated sac-like lobes joined anteriorly by a single commissure. Each lobe is shaped roughly like an L on its side (Figures 5.4 & 5.5) with the anterior of each lobe rounded and upturned. Paired oviducts originate laterally on each side of the commissure and lead ventrally, connecting the organ with the female gonopores on the coxa of the third pereopods. The oviducts have numerous longitudinal folds and are much wider proximally to the ovary (Figures 5.4 & 5.5).

The ovary varies greatly in size and shape depending on the age and reproductive cycle of the female. The changes in the anatomy of the ovary from juvenile to mature female are similar in *Astacopsis* and *Parastacoides* and are summarized below and pictured in Figure 5.4 (Note: the anatomy and development of the ovary in *A. gouldi* and *A. franklinii* Western form are identical to that of *A. franklinii* Eastern form).

Ovaries of the smallest juvenile crayfish are very small and white in colour. They do not have discernible ova but have tiny irregularly shaped white granules within them.

Ovaries of small immature females are small and white in colour with small, very loosely packed, round to oval, white ova without yolk. These ova often appear contained within round, clear envelopes of larger diameter (Fig. 5.4A & E).

Ovaries of larger immature females are yellow in colour (indicating the presence of yolk), small to medium sized, with oval, loosely packed eggs of variable size and yolk content (Fig. 5.4B & F). The body size at which yolky eggs were first noted was CPL 92 in *A. gouldi*, CPL 55 in *A. franklinii* Western form, CPL 37 in *A. franklinii* Eastern form and CPL 22 in *P. t. tasmanicus* (SP). As these females

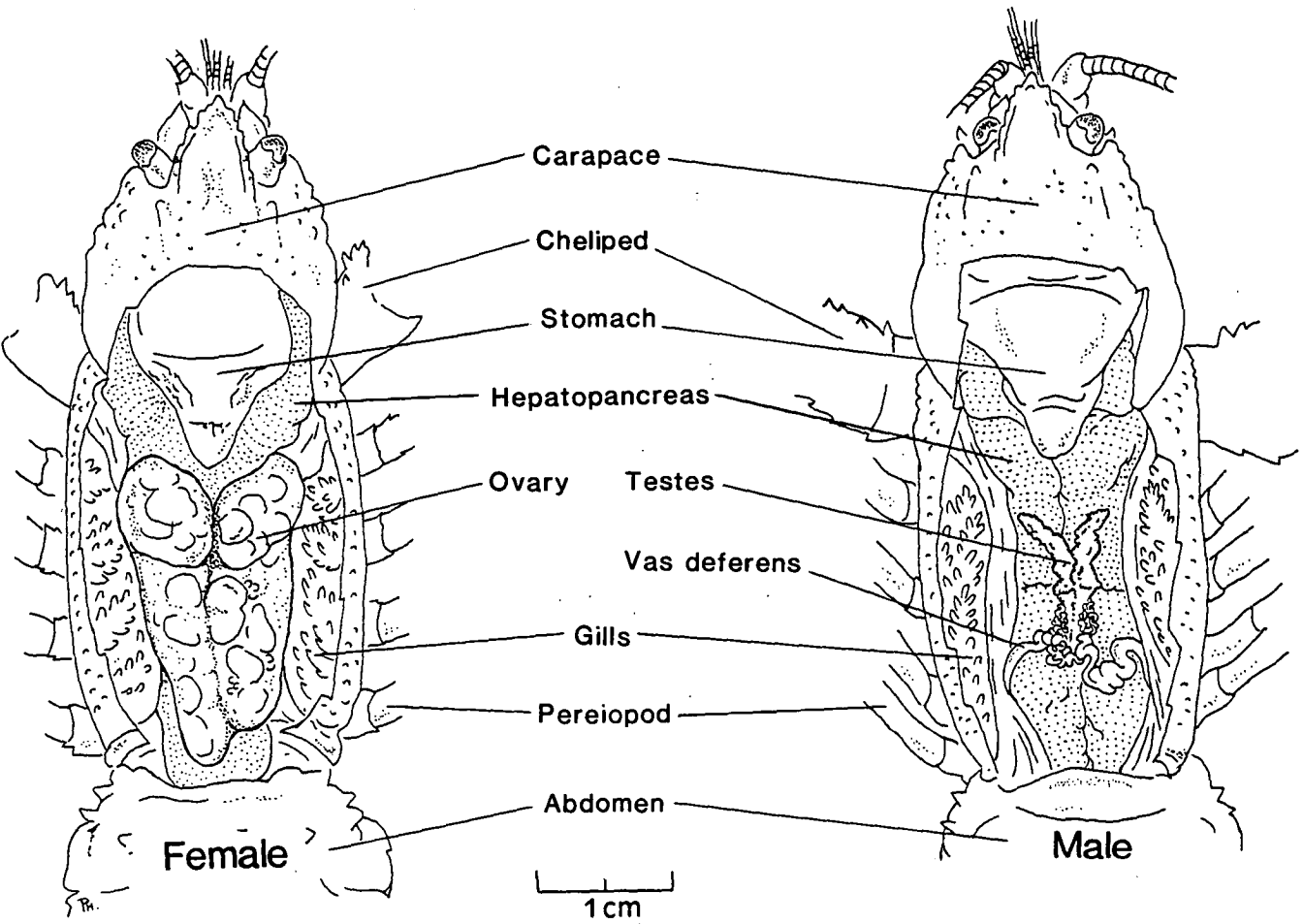


Figure 5.2 Female and male reproductive organs of *Astacopsis franklinii*. Dorsal view with carapace partly cut away, heart and connective tissue removed. Mature crayfishes just prior to mating (April). Male and female CPL 46.0 mm.

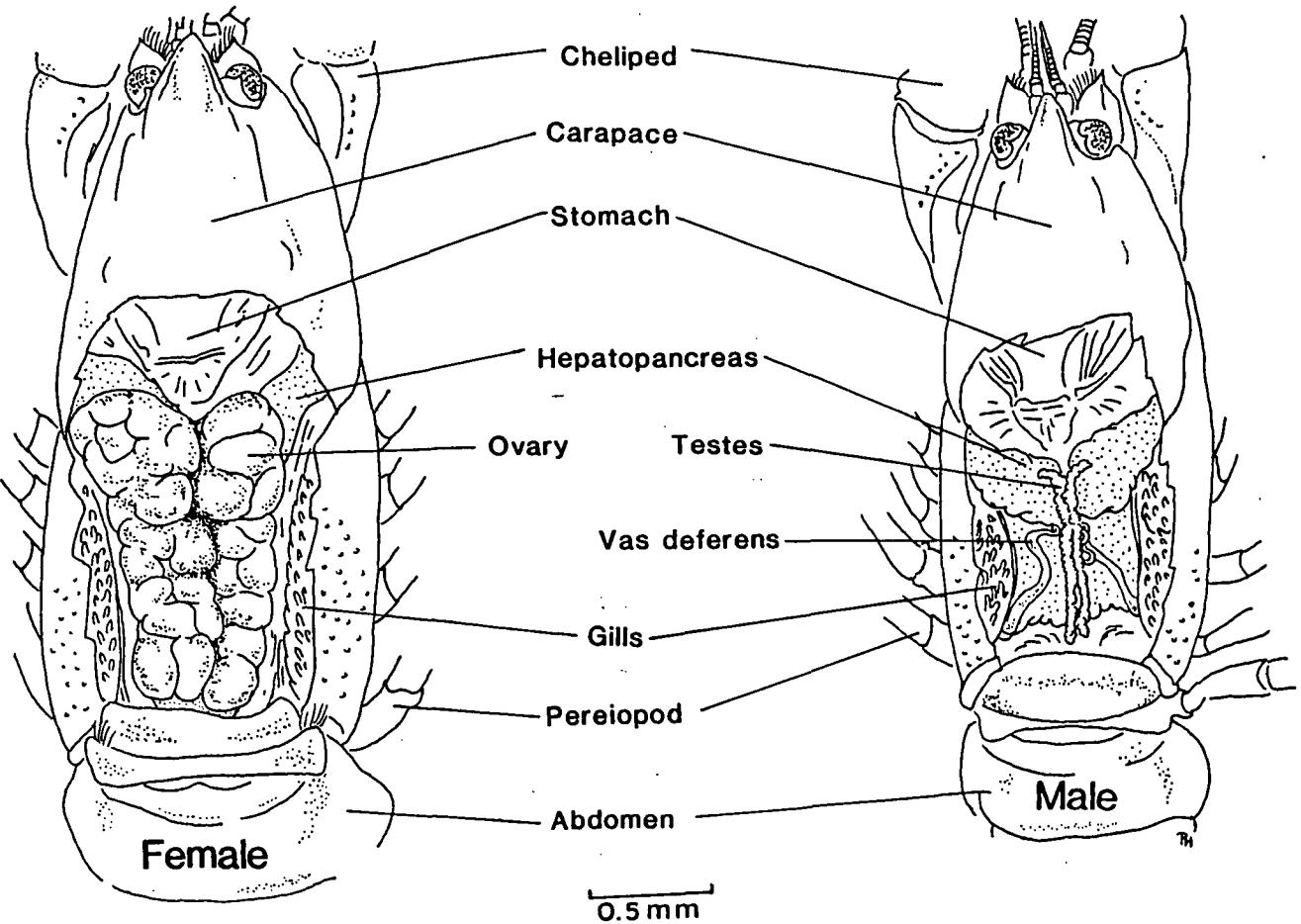


Figure 5.3 Female and male reproductive organs of *Parastacoides tasmanicus*. Dorsal view with carapace partly cut away, heart and connective tissue removed. Mature crayfishes just prior to mating (February). Male CPL 24 mm, female CPL 30.0 mm.

Figure 5.4 Development of female reproductive organs:

***A. franklinii* (Eastern form)**

A. immature female CPL 16.0 mm

B. immature female CPL 29.0 mm

C. maturing female CPL 38.5 mm

D. mature female CPL 45.5 mm (D1 dorsal view, D2 lateral view)

***P. t. tasmanicus* (SP)**

E. immature female CPL 15.5 mm

F. immature female CPL 25.3 mm

G. mature female CPL 30.0 mm (G1 dorsal view, G2 lateral view)

Scale bar indicates actual size of gonad.

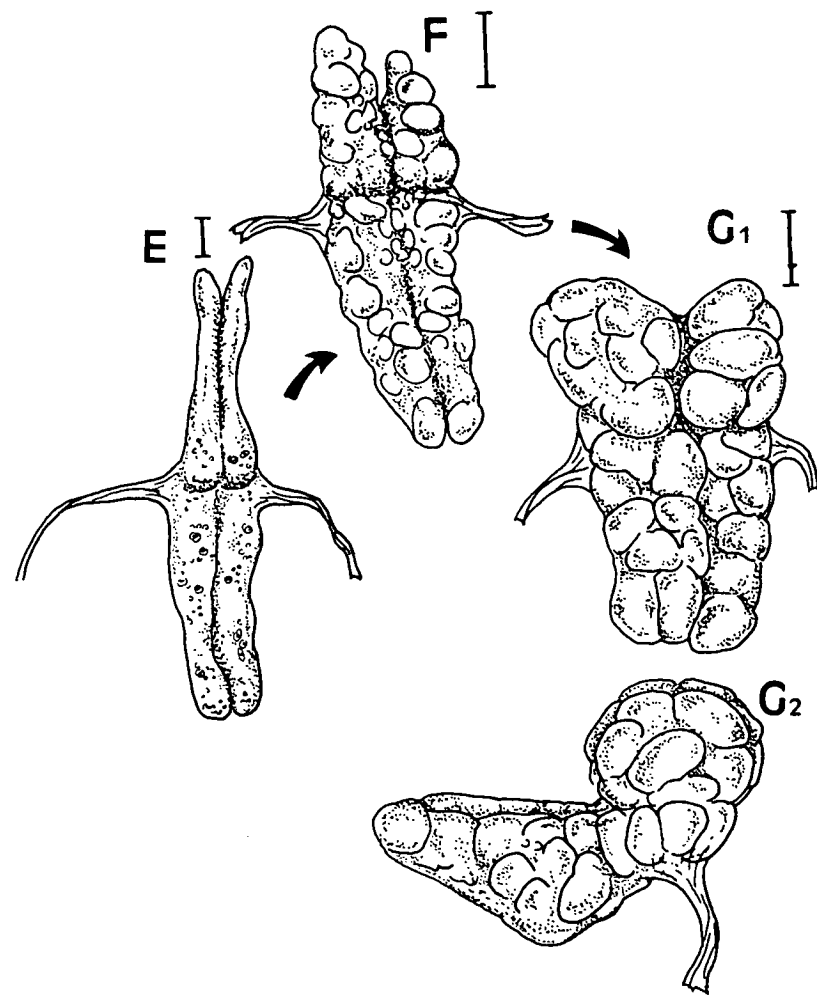
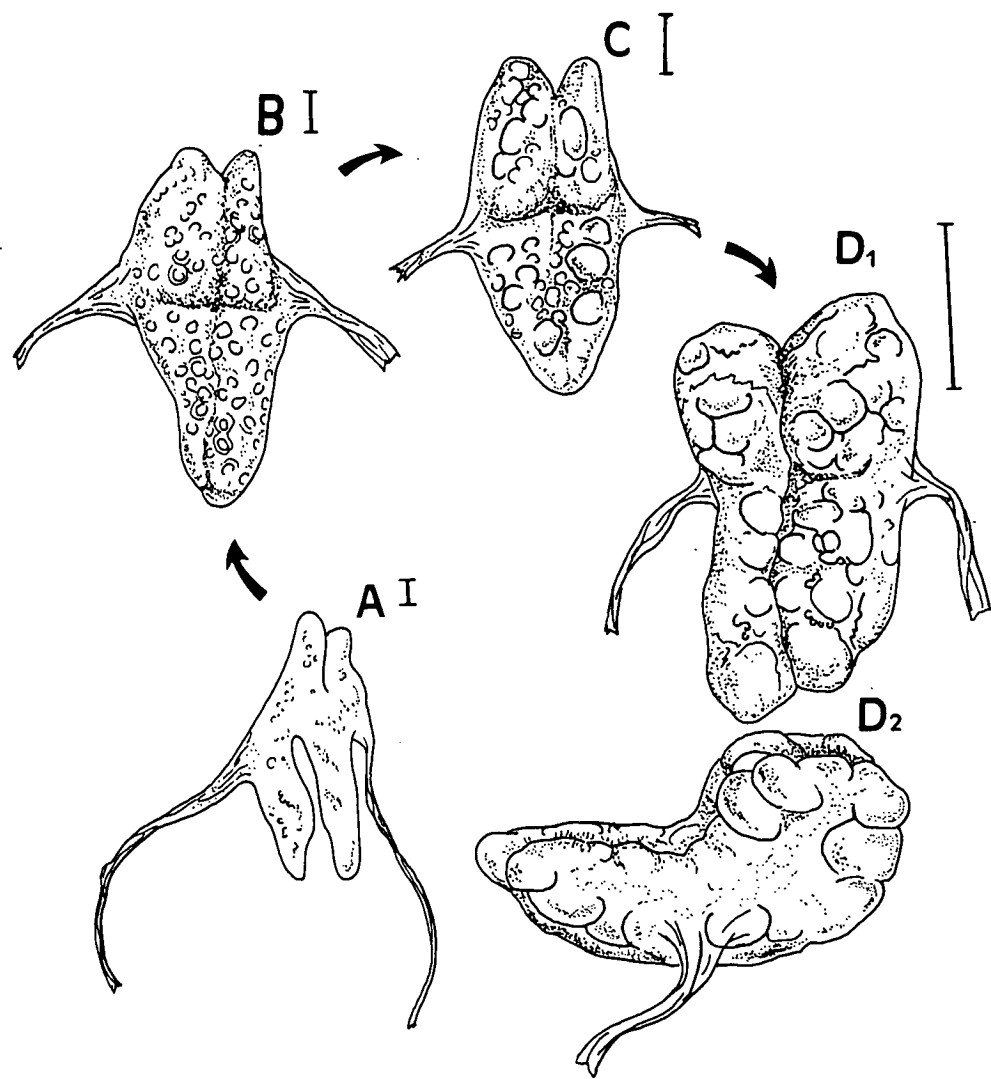


Figure 5.5 Development of male reproductive organs:

***A. franklinii* (Eastern form)**

A. immature male CPL 25.5 mm

B. mature male CPL 40.5 mm

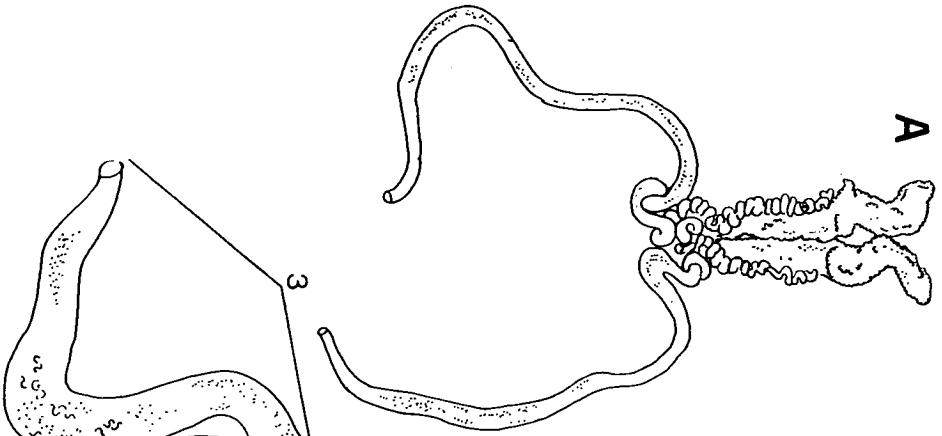
***P. t. tasmanicus* (SP)**

C. immature male CPL 16.0 mm

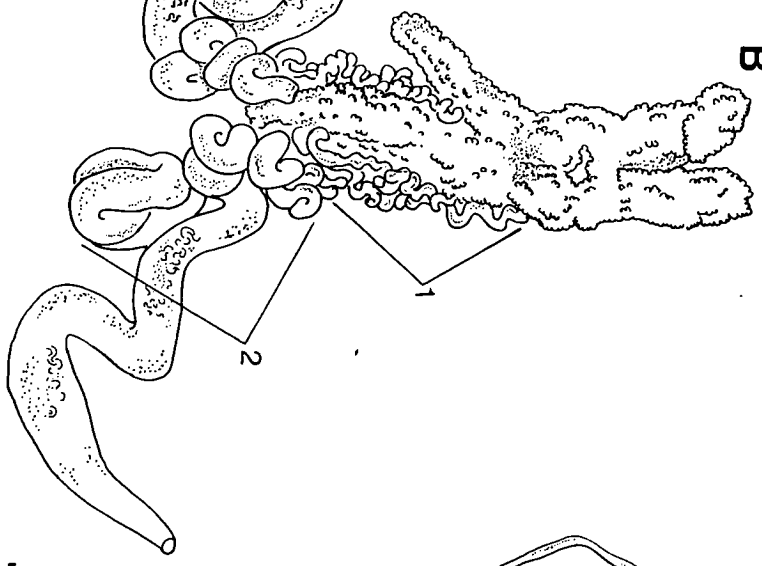
D. mature male CPL 31.5 mm

(regions of vasa deferentia: 1. proximal, 2. middle and 3. distal)

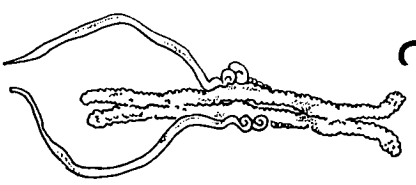
A



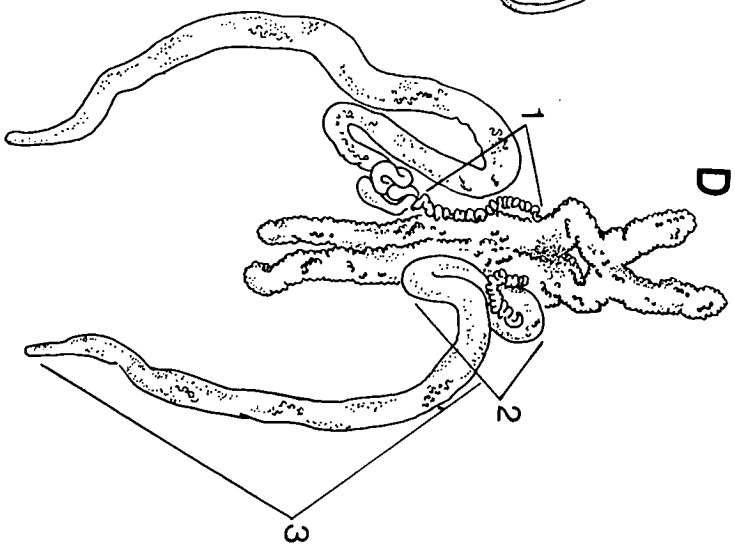
B



C



D



1mm

approach maturity the eggs become more uniform in size and more closely packed, their yolk content increases, their colour darkens and the ovaries take on the proportions seen in mature females.

Ovaries of mature (reproducing) females are large, with large, roughly oval, tightly packed eggs with a high yolk content (Figure 5.4 D & G). Mature ova (ie: just prior to extrusion) are dark brown in *Astacopsis* spp. (almost black in *A. gouldi*), light brown in *Parastacoides t. tasmanicus* (SP), while in *P. t. inermis*, *P. t. insignis* and *P. t. tasmanicus* (N) and (I) they are bright yellow.

B. The male gonad:

The testes of *Astacopsis* and *Parastacoides* are located within the cephalothorax, between the second and fourth pereopods. They are smaller and much less conspicuous than the female organ, resting snugly on top of the hepatopancreas, posterior to the stomach and directly below the heart (Figures 5.2 & 5.3). The testis is roughly H shaped consisting of two cylindrical lobes joined anteriorly by a small transverse commissure. The anterior parts of the lobes are shorter and face dorsally, resting up against the inner surface of the carapace just behind the cephalic groove. The posterior lobes are longer and, in *Parastacoides*, run posteriorly as far as the first abdominal segment. The surface of the testicular lobes consists of very small globules resembling bunches of grapes. When examined microscopically, it becomes evident that the testis is made up of sperm-producing acini connected by tubules to the main trunk of the testis.

The paired vasa deferentia emerge laterally a short distance from the transverse commissure. Each vas deferens can be divided into the three following regions (Fig. 5.5):

1. A proximal, highly convoluted portion with a small diameter consisting of small, tight coils, in close proximity to the testis.
2. A middle section with a larger diameter and large, loose coils.
3. A distal section with a yet larger diameter, without coils, curving ventrally to open into the gonopores on the coxa of the fifth pereopods.

In *Astacopsis* the proximal and middle sections are longer and more convoluted than in *Parastacoides* (Fig. 5.5B & D). The posterior lobes of the testes are also less distinct from each other in *Astacopsis* and do not extend past the first coils of the

middle section of the vas deferens (Fig. 5.5B & D). In adult *A. franklinii* Eastern form, there appears to be an additional lobe of the testis which emerges from the left posterior lobe just above the origin of the vas deferens (Fig. 5.5B). This feature of the male gonad was not observed in either *A. franklinii* Western form or *A. gouldi* but otherwise gonad morphology appeared identical in the three *Astacopsis* examined (see Fig. 6.5 for diagram of *A. gouldi* testes).

The testis varies in size and shape depending on the age and reproductive cycle of the male. The changes in the anatomy of the male gonad from juvenile to mature individuals are similar in *Astacopsis* and *Parastacoides* as pictured in Figure 5.5. In mature males, the gonads are generally much larger, the lobes of the testes are thicker and longer, while the vas deferens is more convoluted, thicker, with a larger diameter when compared to the immature gonads. Spermatophores with coiled sperm tubes can be seen in the vas deferens of mature reproducing males but are not present at any time in immature individuals (see Chapter 6). Spermatozoa contained within the tubes are round, conspicuously nucleated and lacking the rays characteristic of the sperm of other Astacidea. The testes of both genera are white in colour at all stages in development.

5.3.2 Morphology and development of genitalia

A. The female gonopore:

Astacopsis: The female gonopores are a pair of oval openings on the ventral surfaces of the coxae of the third pereopods. In mature females the openings are closed by a decalcified, slightly convex membrane and surrounded by a very dense ring of setae (Figs. 5.6G, 5.7D & 5.8E). During egg extrusion, the gonopore cover collapses posteriorly to reveal the oviduct. In immature females the openings are simple, without sculpturing or setation, and are closed over by a flat, calcified cover. As the females grow toward maturity the gonopores increase in size and a raised, ring-like rim, bearing setae, forms around the opening, whose cover becomes progressively decalcified (Figs. 5.6A-F, 5.7A-C & 5.8D-E). The setal ring is lost and regained through a molt during the reproductive cycle of mature females (Figs. 5.6G-H, 5.7D-E). This phenomenon is discussed in more detail in Chapter 6.

The smallest female with a completely decalcified gonopore cover and

Figure 5.6 Development of female gonopores in *A. gouldi*:

- A.** CPL 16.5 mm, immature female: hard, closed cover, no or few setae.
- B.** CPL 34.5 mm, immature female: as above.
- C.** CPL 46.0 mm, immature female: as above.
- D.** CPL 86 mm, immature female: as above.
- E.** CPL 111.0 mm, immature female: as above.
- F.** CPL 119.5 mm, maturing female: cover softening, setose.
- G.** CPL 134.5 mm, mature female, reproductive condition: soft cover, heavily setose.
- H.** CPL 131 mm, mature female, nonreproductive condition: soft cover, setae lost.

Scale bar = 1 mm

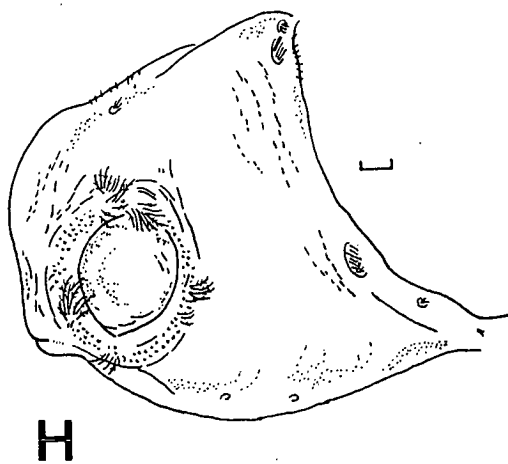
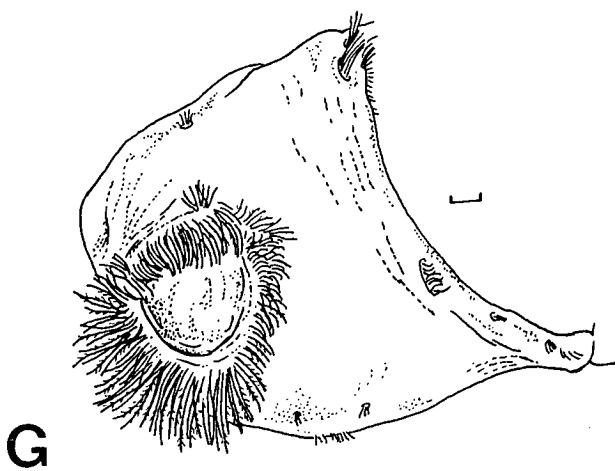
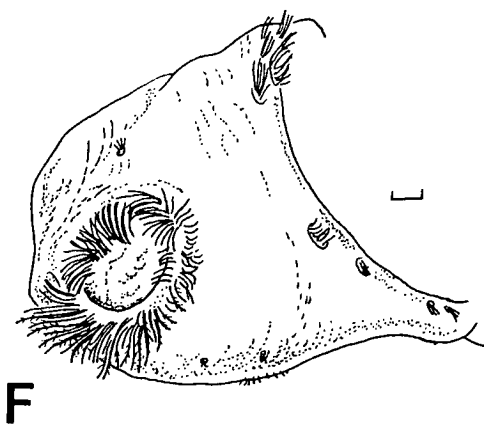
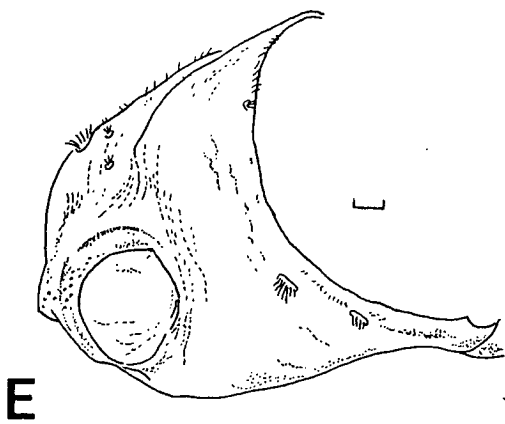
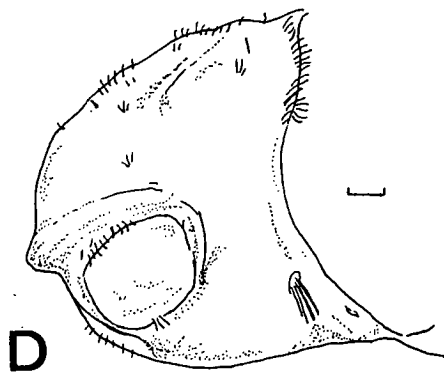
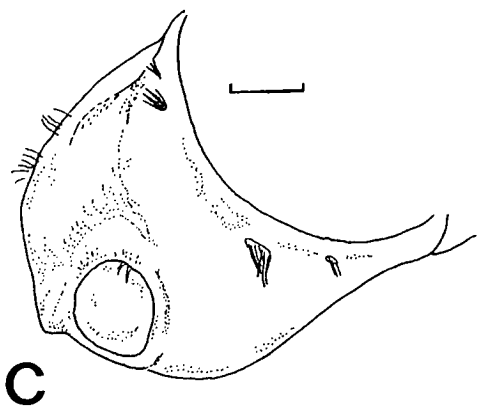
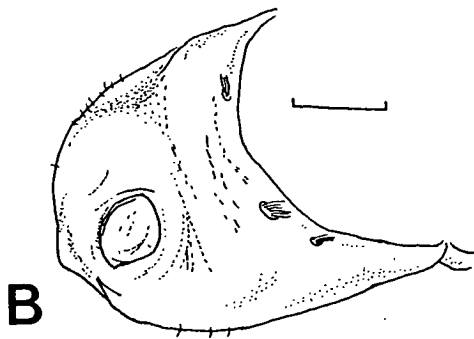
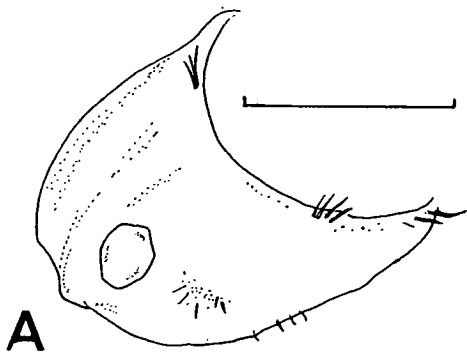
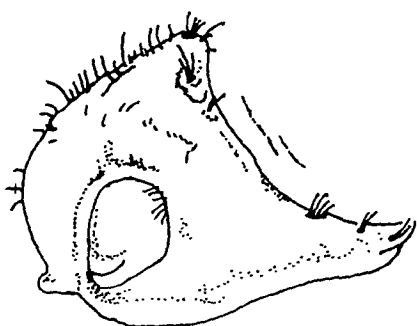
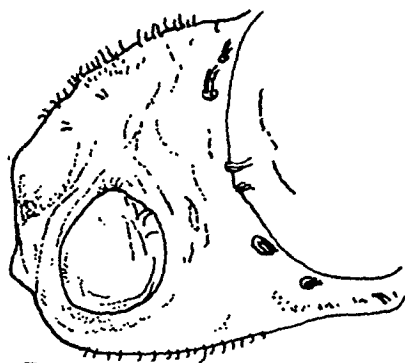


Figure 5.7 Development of female gonopores in *A. franklinii*
(Eastern form)

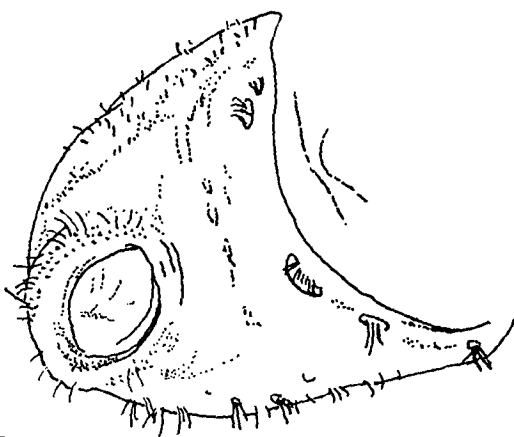
- A.** CPL 19.0 mm, immature female: hard, closed cover, no setae.
- B.** CPL 37.0 mm, immature female: as above.
- C.** CPL 43.0 mm, maturing female: cover softening, few setae.
- D.** CPL 45.5 mm, mature female, reproductive condition: soft cover, heavily setose.
- E.** CPL 45.5 mm, mature female, nonreproductive condition: soft cover, setae lost.



A



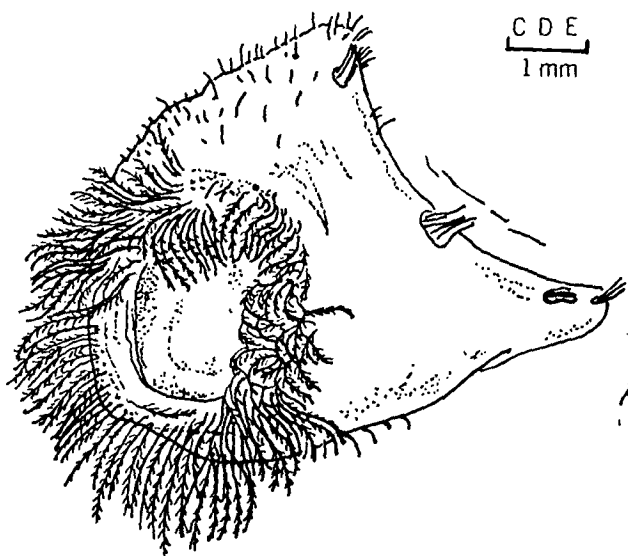
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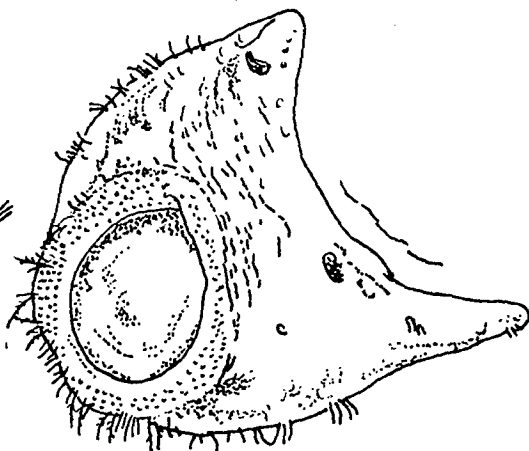
C

A B
1 mm

C D E
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D



E

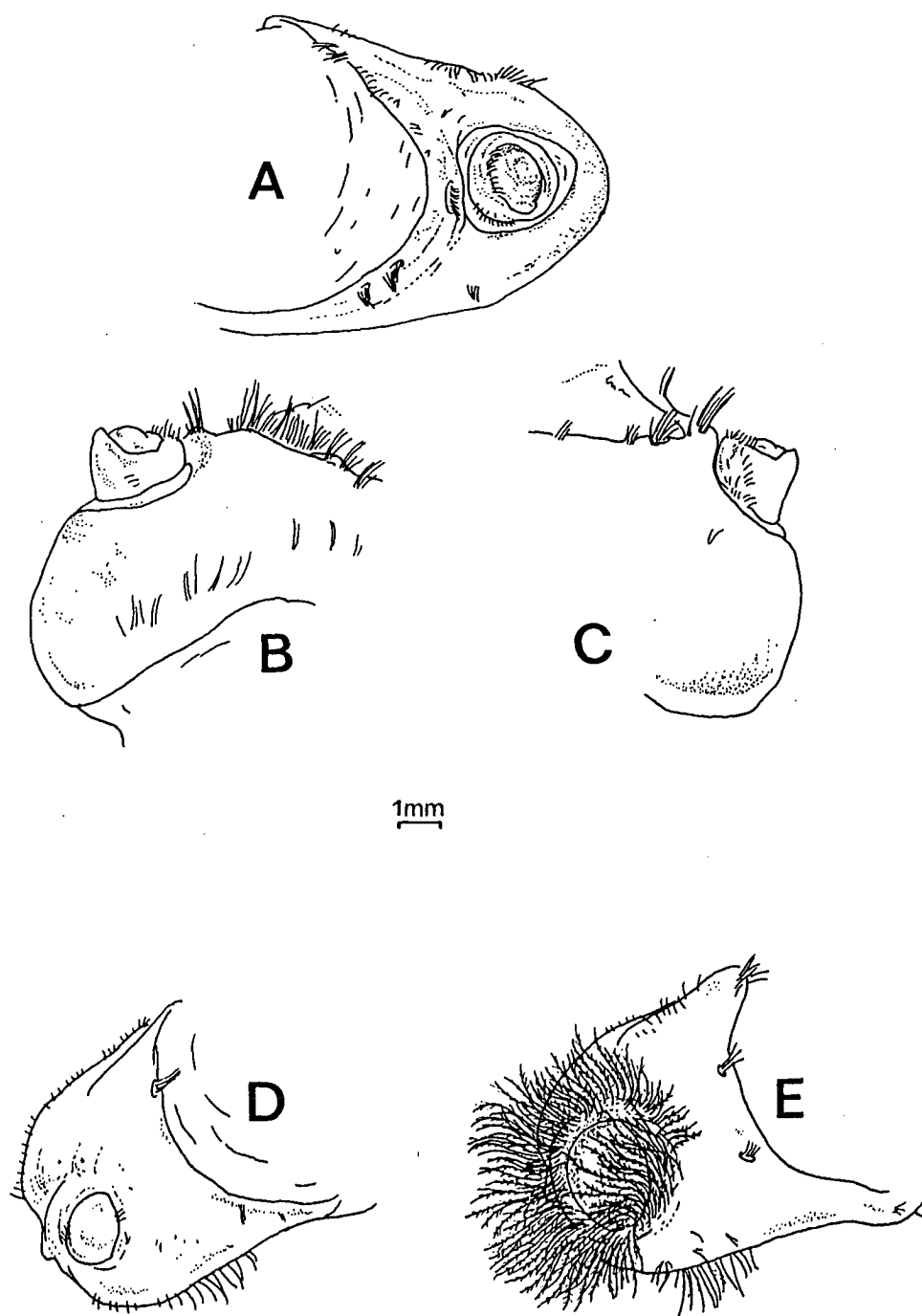


Figure 5.8 Male and female gonopores of *A. franklinii* (Western form) from Lake Meston.

A. - C. Mature male, CPL 87.6 mm (A. ventral view, B. cephalic view, C. caudal view)

D. Immature female, CPL 64.5 mm, hard cover, nonsetose.

E. Mature female, CPL 80.3 mm,; soft cover, heavily setose.

heavy setal fringe measured 118.6 mm CPL in *A. gouldi*, 62 mm CPL in *A. franklinii* Western form and 38.5 mm CPL in *A. franklinii* Eastern form while the largest female with a nonsetose calcified gonopore measured 118.5 mm CPL in *A. gouldi*, 58 mm CPL in *A. franklinii* Western form and 45.5 mm CPL in *A. franklinii* Eastern form.

Changes in the dimensions of the genital apertures related to body size in *A. gouldi*, *A. franklinii* Eastern form and *A. franklinii* Western form are shown in Figure 5.9. Gonopore dimensions in *Astacopsis* increase linearly with respect to carapace length. In *A. franklinii* Eastern form, gonopores are larger for a given size of female than in the other two species. When the gonopore length to gonopore width ratios of the two forms of *A. franklinii* were compared statistically, a significant difference was found ($t = 3.4$, $df = 97$, $p < 0.001$). In all three *Astacopsis* species/forms the gonopores are rounder in small individuals and become progressively more ovoid in older individuals. No significant change in the relationship between gonopore dimensions and the attainment of maturity was detected in *A. gouldi* or *A. franklinii*.

Parastacoides: The female gonopores are a pair of oval openings on the ventral surfaces of the coxae of the third pereopods. In mature females the openings are closed over by a decalcified, slightly convex membrane and partially surrounded by a fringe of setae (Figs. 5.10H and 5.11D&H). The opening mechanism of the gonopores is identical to that of *Astacopsis*. In immature females the openings are simple, without sculpturing or setation, and are closed-over by a calcified cover. As the females grow toward maturity the gonopores increase in width and length, and setae appear on the edge of the opening, whose cover becomes progressively decalcified (Figs. 5.10F-G). The smallest female of *P. t. tasmanicus* (SP) with a decalcified and setose gonopore measured 23.6 mm CPL while the largest female with a nonsetose calcified gonopore measured 29.8 mm. The setae of mature females are not lost during the reproductive cycle as in *Astacopsis* (Figs. 5.10H-I).

Changes in the dimensions of the gonopores related to carapace length in *P. t. tasmanicus* (SP) are shown in Figure 5.11. The female gonopores of mature *P. t. tasmanicus* (SP) are shown in Figure 5.11. The female gonopores of mature *P. t. inermis* and *P. t. insignis*, although generally similar, differ from *P. t. tasmanicus* (SP) in the setation around the gonopore. In *P. t. tasmanicus* (SP) the fringe is limited to the anterior edge of the gonopore (Fig. 5.10H) while in the other two subspecies the fringe extends ventrally along the outer edge (Figs. 5.12D&H). The

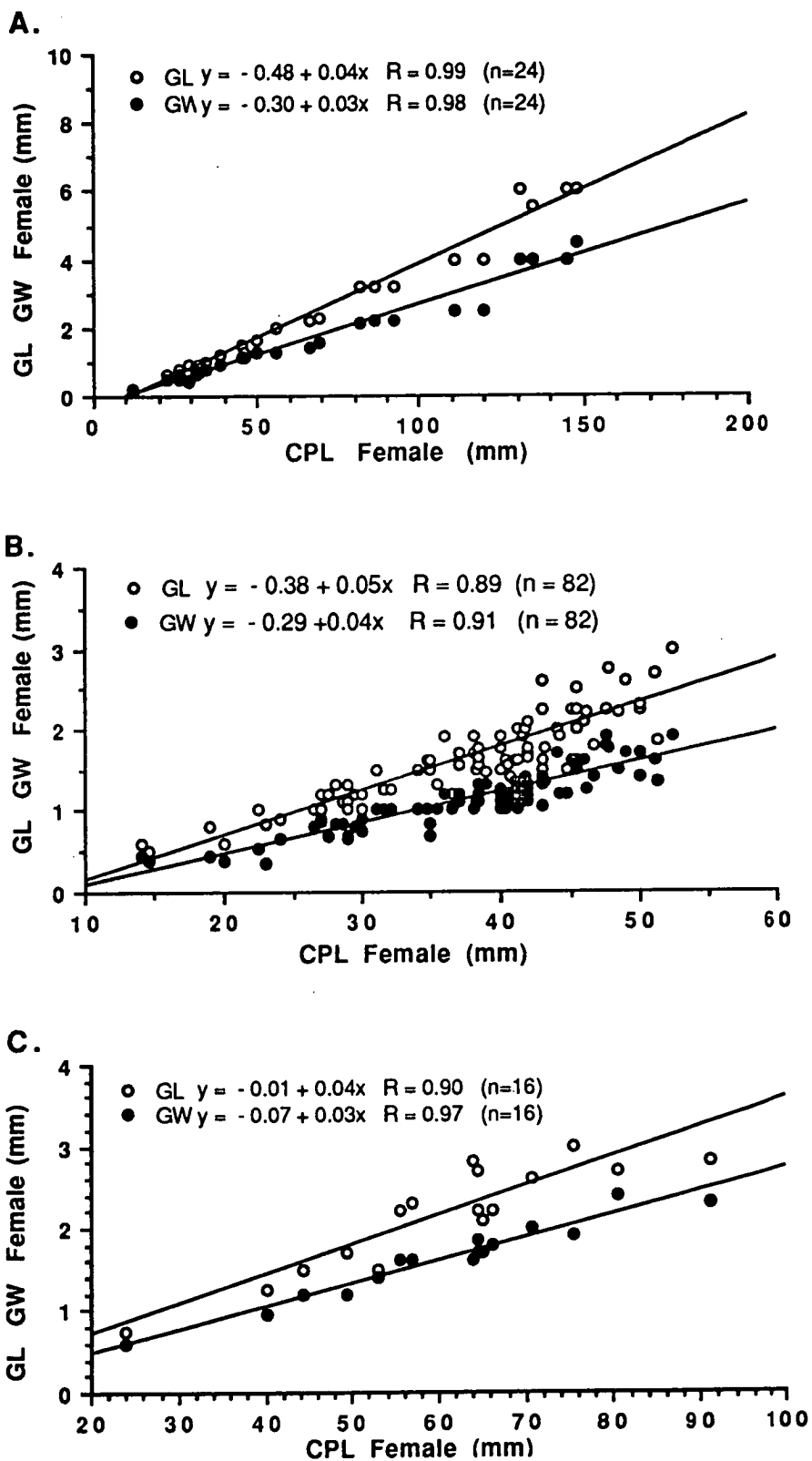


Figure 5.9 The relationship between female gonopore dimensions (length and width) and carapace length.

A. *A. gouldi*

B. *A. franklinii* (Eastern form)

C. *A. franklinii* (Western form)

Figure 5.10 Development of male and female gonopore in *P. t. tasmanicus* (SP) from Harlequin Hill:

1. Immature male, CPL 12.0 mm.

2. Mature male, CPL 33.0 mm.

(**A.** ventral view; **B.** cephalic view; **C.** caudal view)

D. Open gonopore of mature male.

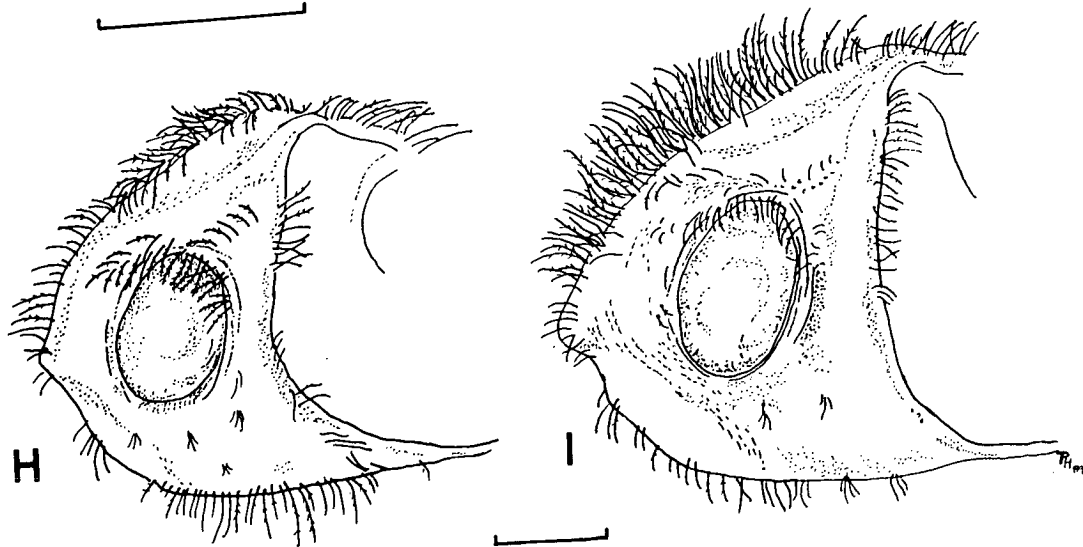
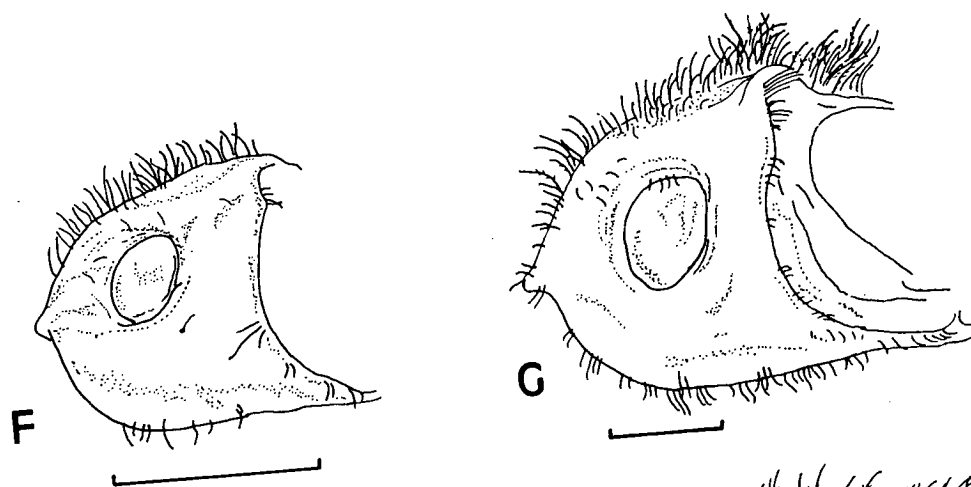
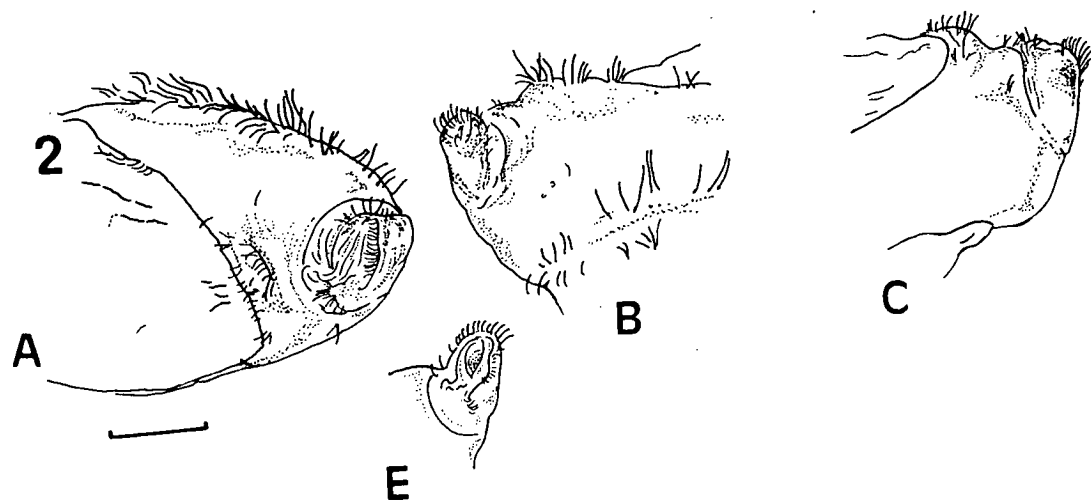
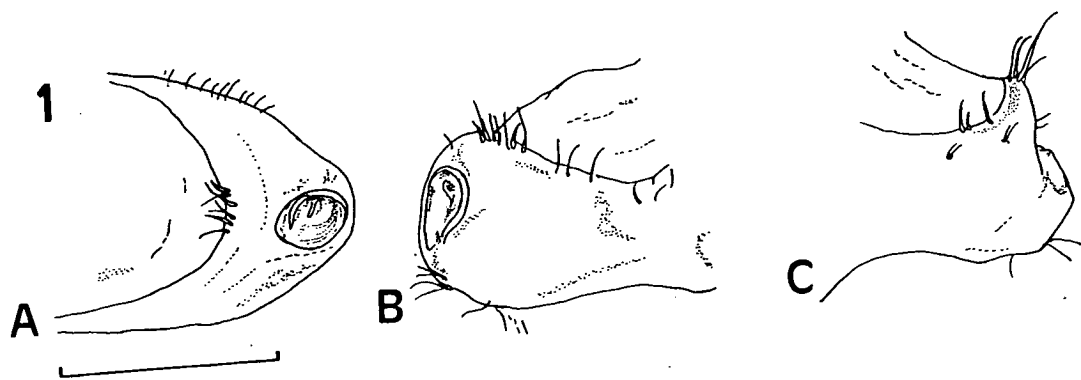
E. Immature female, CPL 11.7 mm, hard cover few setae.

F. Immature male, CPL 27.0 mm, hard cover few setae.

G. Mature female, reproductive, CPL 30.0 soft cover lightly setose.

H. Mature female, nonreproductive, CPL 32.0 soft cover lightly setose.

Scale bar = 1 mm.



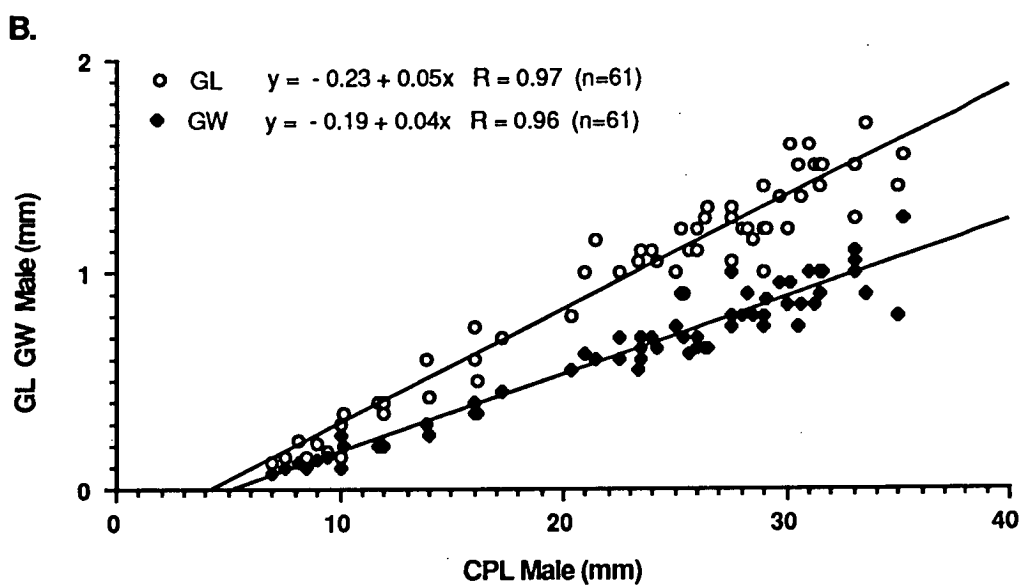
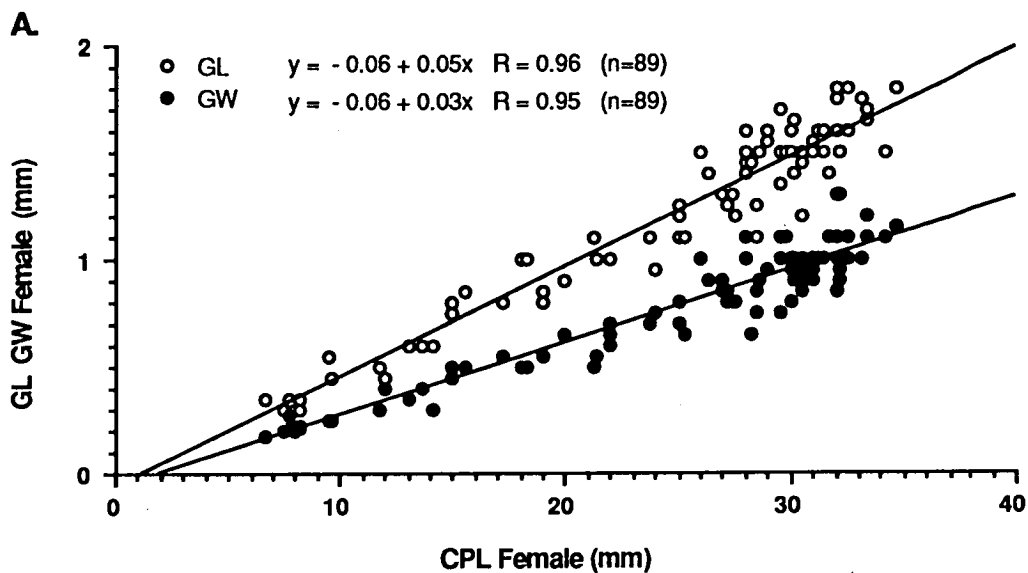


Figure 5.11 The relationship between the length (GL) and width (GW) of the gonopore and carapace length in *P. t. tasmanicus* (SP).

A. Female

B. Male

Figure 5.12 Development of male and female gonopore in *P. t. insignis* and *P. t. inermis*:

A. - C. *P. t. insignis*, mature male, CPL 27.5 mm.

(**A.** ventral view; **B.** cephalic view; **C.** caudal view)

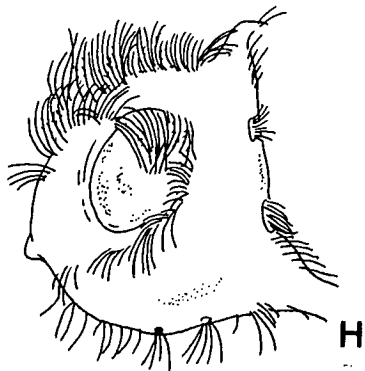
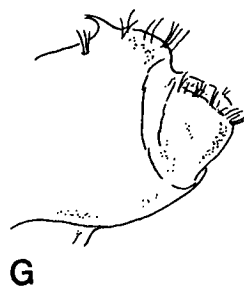
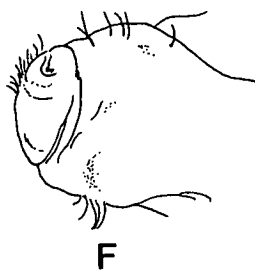
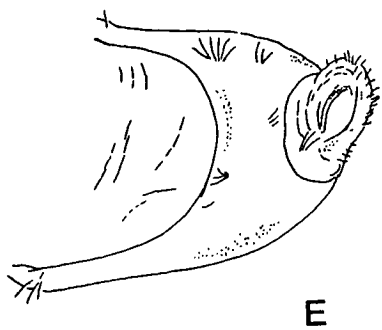
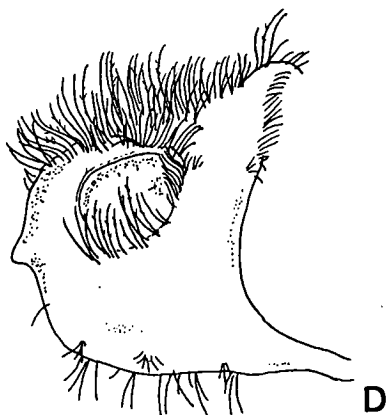
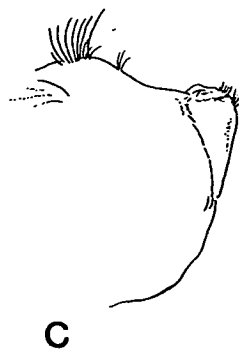
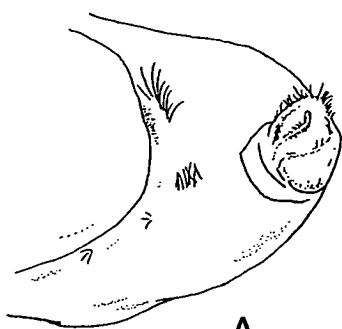
D. *P. t. insignis*, mature female, CPL 27.0 mm.

E. - G. *P. t. inermis*, mature male, CPL 24.0 mm.

(**E.** ventral view; **F.** cephalic view; **G.** caudal view)

D. *P. t. inermis*, mature female, CPL 25.5 mm.

Scale bar = 1 mm.



gonopore setation of *P. t. tasmanicus* (I) and *P. t. tasmanicus* (N) was also found to be similar to that observed on *P. t. inermis* and *P. t. insignis*. Limited morphometric data collected for *P. t. inermis* and *P. t. insignis* suggests that when compared to *P. t. tasmanicus* (SP), *P. t. insignis* has gonopores of similar dimensions while *P. t. inermis* has somewhat larger gonopores at a given size.

B. The male gonopore:

Astacopsis: The male gonopores consist of a pair of raised, sclerotized papillae on the ventral surfaces of the coxae of the fifth pereopods. In adult males the papilla consists of a calcified tube separated from the hard portion of the coxopodite by a membrane (Figs. 5.13/5, 5.14/4 and 5.8A-C). There is no connection between this "papillar" membrane and the arthrodial membrane (membrane between the coxopodite and the first segment of the walking leg). The papilla is closed off at its apex by a concave membrane which closes tightly against a membranous lip on the anterior edge of the papillar tube. During ejaculation, the gonopore opens anteriorly by the backward collapse of the apical membrane, away from the lip (Fig. 5.14/5). The outer surface of the papillar tube and the apical membrane bears short setae in adult specimens. Figures 5.13 and 5.14 show the development of the morphological characters of the male gonopore from juvenile to adult for *A. gouldi* and *A. franklinii*, respectively. In immature individuals the papillar tube is shorter, less sculptured, with few setae and, in very small individuals, the papillar membrane surrounding it is absent. As the juveniles grow, the tube sculpturing as well as setation increases and the papillar membrane develops gradually (Fig. 5.13/1-3). The smallest specimen with a complete membrane was CPL 34.5 mm in *A. gouldi* and CPL 16 mm for *A. franklinii*.

Subtle differences are found in the morphology of the papillae in adult males of the three species/forms: In *A. gouldi* the separation between the papillar membrane and the arthrodial membrane is very narrow, while in both forms of *A. franklinii* it is relatively wide. The papillar tube of *A. franklinii* Western form, when compared to that of the Eastern form, is more cylindrical, less sculptured and has a raised inner edge (Figs. 5.14/5, 5.8A-C and 5.13/4).

Changes in the dimensions of the gonopores related to body size in *A. gouldi*, *A. franklinii* Eastern form and *A. franklinii* Western form are shown in Figure 5.15. Gonopore dimensions in *A. gouldi* as well as both *A. franklinii* Forms increase

Figure 5.13 Development of male gonopore in *A. gouldi*:

1. Immature male, CPL 12.2 mm.
2. Immature male, CPL 20.5 mm, papillar membrane begins to form.
3. Immature male, CPL 23.3 mm, papillar membrane forming.
4. Immature male, CPL 63.0 mm, papillar membrane fully formed.
5. Mature male, CPL 181.0 mm.

(**A.** ventral view; **B.** cephalic view; **C.** caudal view)

Scale bar = 1 mm.

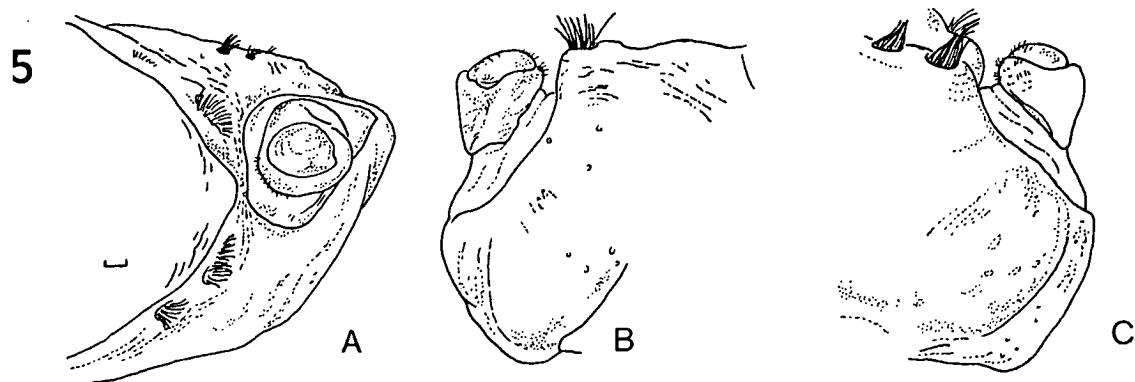
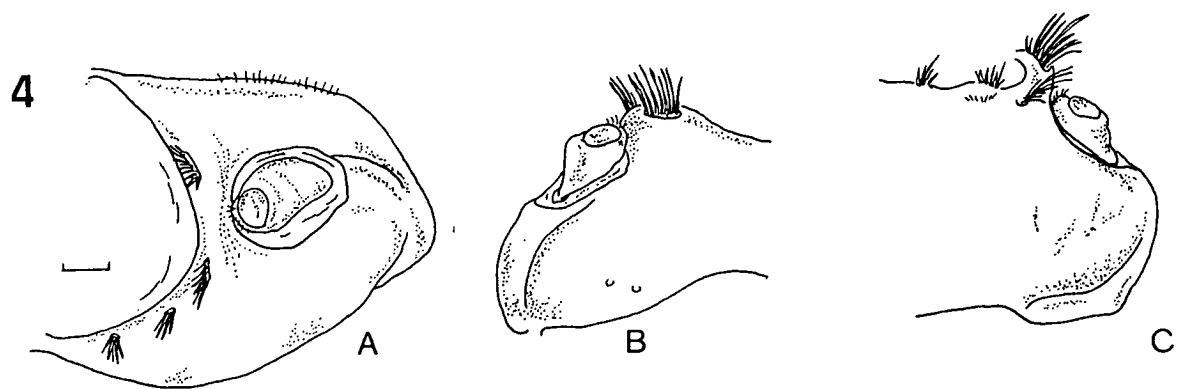
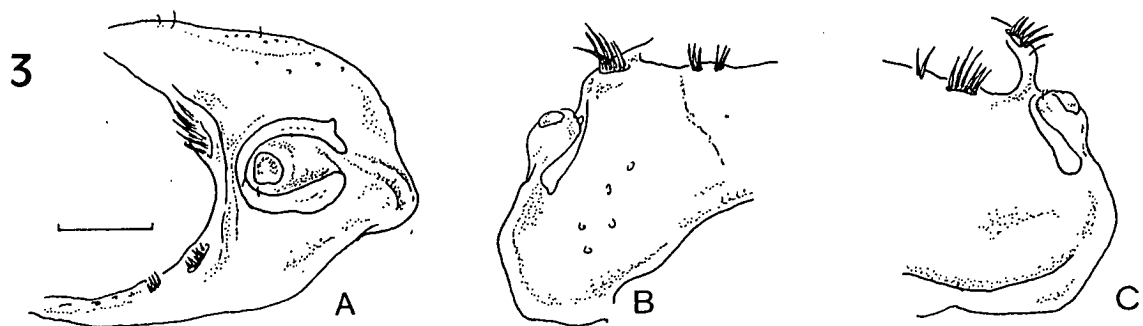
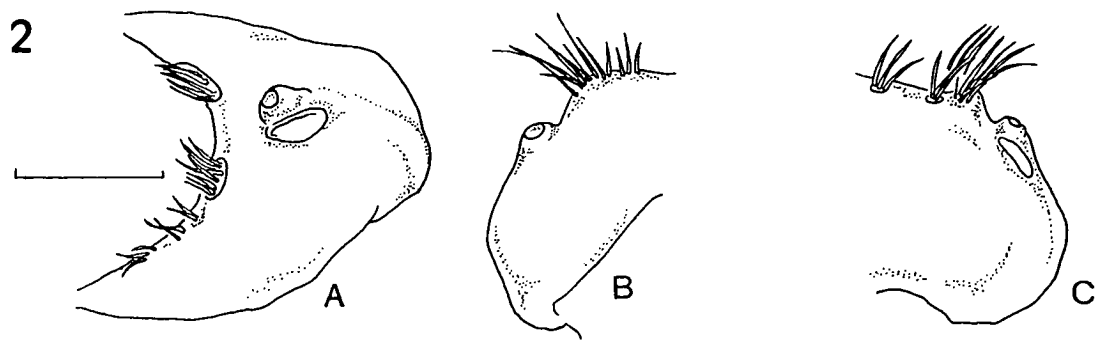
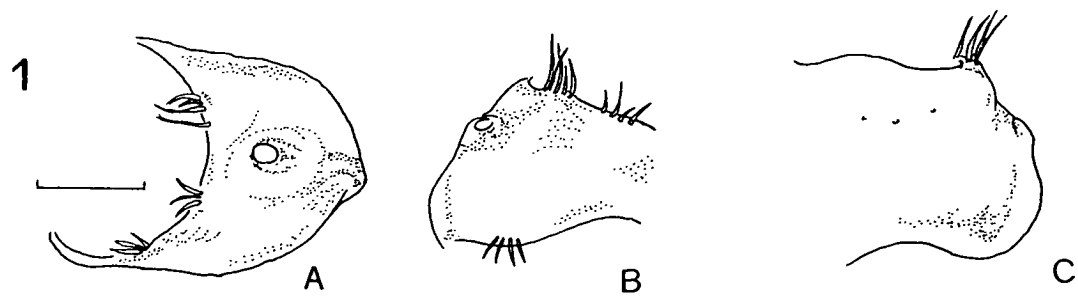


Figure 5.14 Development of male gonopore in *A. franklinii*

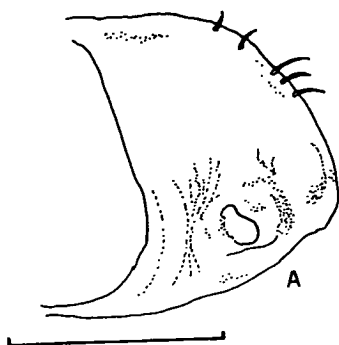
(Eastern form):

1. Immature male, CPL 8.5 mm.
2. Immature male, CPL 16.5 mm
2. Immature male, CPL 25.5 mm
4. Mature male, CPL 46.0 mm.
5. Open gonopore of mature male (am = apical membrane, l = lip).

(A. ventral view; B. cephalic view; C. caudal view)

Scale bar = 1 mm.

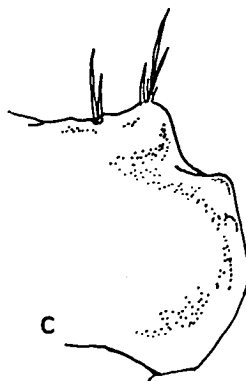
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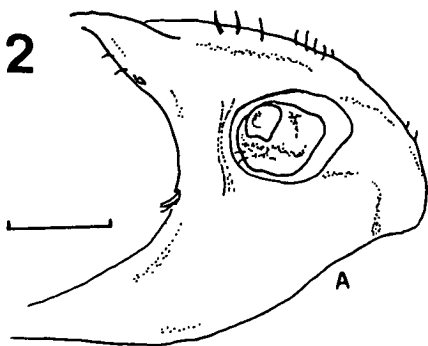
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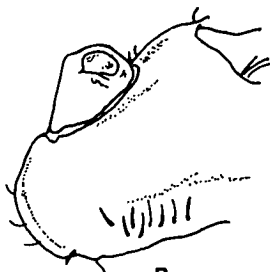
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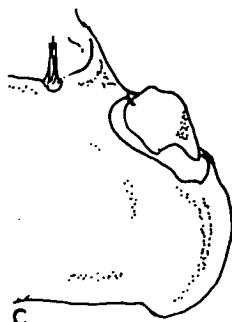
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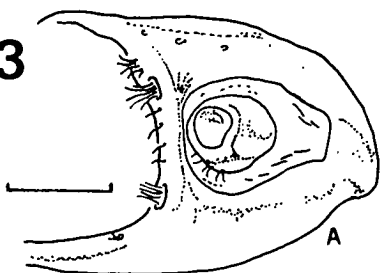
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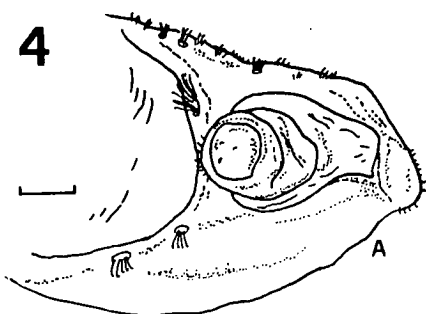
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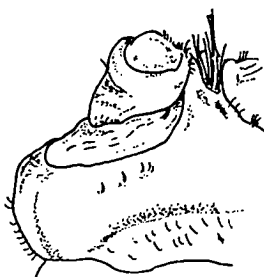
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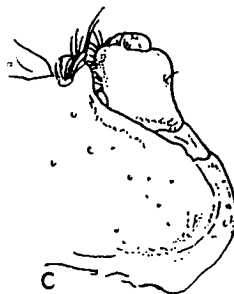
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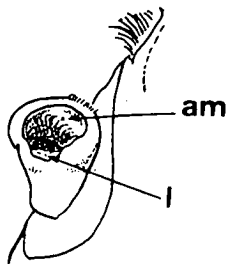


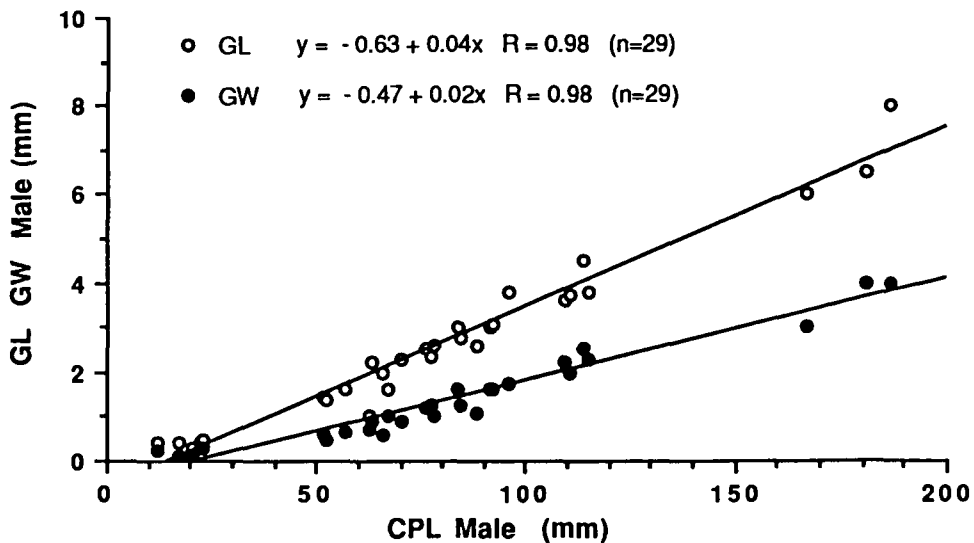
Figure 5.15 The relationship between the length (GL) and width (GW) of the male gonopore and carapace length in :

A. *A. gouldi*

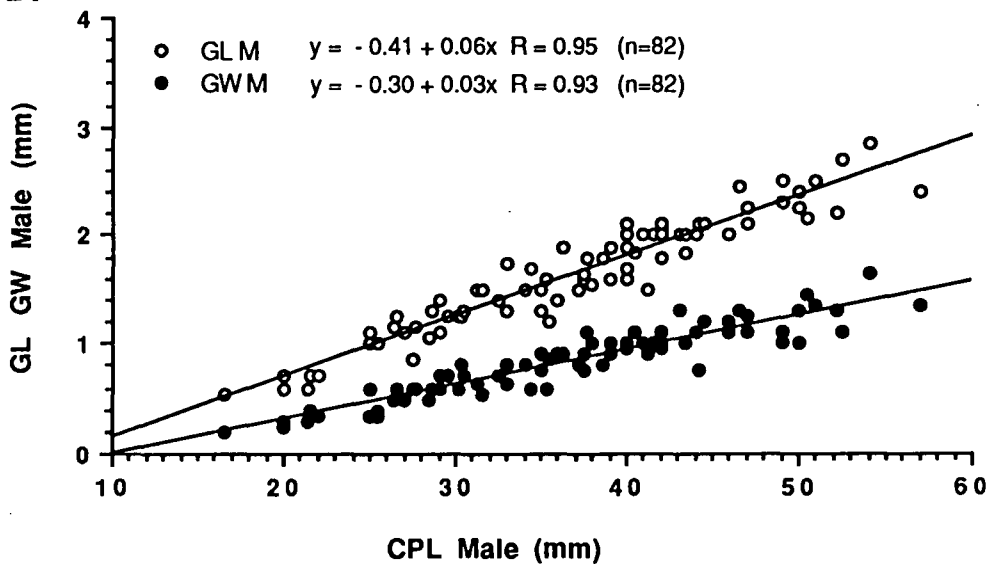
B. *A. franklinii* (Eastern form).

C. *A. franklinii* (Western form).

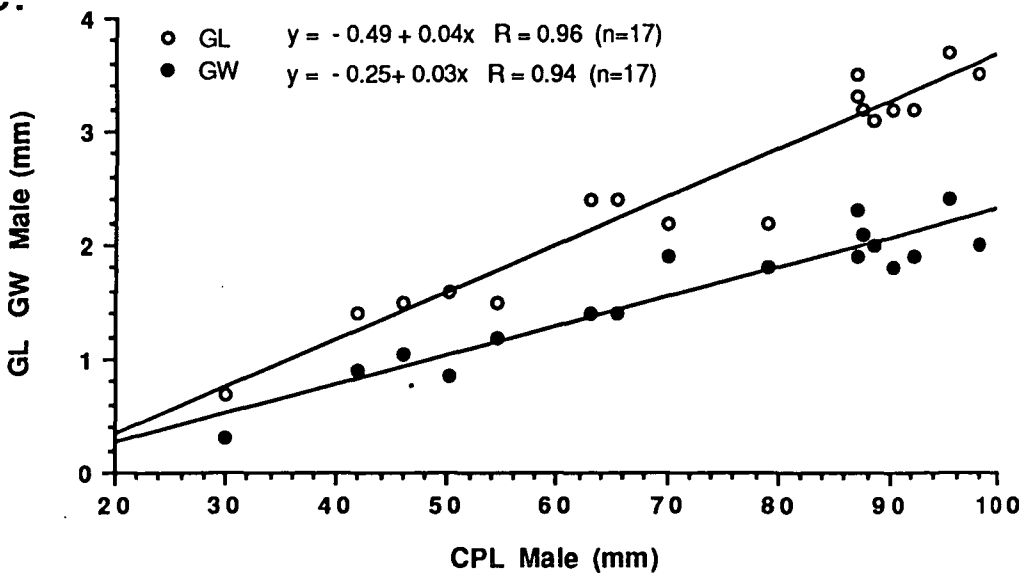
A.



B.



C.



linearly with respect to carapace length. In *A. gouldi* and *A. franklinii* Western Form the gonopores have similar dimensions, while in *A. franklinii* Eastern Form the papillae are longer for a given size of male than in the other two species. No significant change in the relationship between gonopore dimensions and the attainment of maturity was detected in *A. gouldi* or *A. franklinii*.

Parastacoides: The male gonopores consist of a pair of raised, weakly calcified, membranous papillae on the ventral surfaces of the coxae of the fifth pereopods. There is no calcified ring and the papilla has a pointed, triangular appearance. In adult males the papilla consists of a weakly calcified U shaped section which is embedded in, and continuous with, the surrounding papillar membrane (Figs. 5.10/2, 5.12A-C & E-G). The papillar membrane and the arthrodistal membrane are separate. Unlike *Astacopsis*, the papilla opens at its apex by a median suture, surrounded by a raised lip on either side (Fig 5.10E). During ejaculation the lips open laterally to reveal the distal end of the vas deferens. The apex of the papilla is surrounded by short setae in adults. In immature individuals the papillae are smaller, less complex and lacking setae (Fig. 5.10/1). There were no major morphological differences noted in the gonopores of mature *P. t. inermis*, *P. t. insignis* and *P. t. tasmanicus* (SP) (Fig. 5.12A-C & E-G).

Changes in the dimensions of the gonopores related to body size in *P. t. tasmanicus* (SP) are shown in Figure 5.11B. No significant change in the relationship between gonopore dimensions and the attainment of maturity was detected in *Parastacoides*. Limited morphometric data collected for *P. t. inermis* and *P. t. insignis* suggests that when compared to *P. t. tasmanicus* (SP), *P. t. insignis* has gonopores of similar dimensions, while *P. t. inermis* has somewhat larger gonopores at a given size.

C. Intersexuality

Intersex individuals were very rare in *Astacopsis* and *Parastacoides*. None of the *Astacopsis* caught exhibited the intersex condition (both male and female gonopores present).

In *Parastacoides*, only three intersex individuals were found. They were a *P. t. tasmanicus* (SP) (CPL 26.2 mm) with a male gonopore on the left side and a female gonopore on the right side and two *P. t. inermis*, (CPL 20.4 mm and 24.5 mm) with both male and female gonopores. The later of the two *P. t. inermis* was

a functional female carrying a fertile brood of eggs. This accounted for 0.03 percent of the total number caught in *P. t. inermis* and 0.001 percent in *P.t. tasmanicus*.

5.3.3 Secondary sexual characters / sexual dimorphism

A. Glair glands

Astacopsis: Glair glands are small, creamy white circular glands which can be seen ventrally in the abdomens of sexually mature females prior to, and at the time of, reproduction (see Chapter 6). These glands are thought to produce the cement which attaches the eggs to oostetae of the female pleopods (Stephens, 1952; Yonge, 1937; Aiken & Waddy, 1982).

The glair glands of *A. gouldi* and *A. franklinii* underlie the abdominal sterna extending laterally into the associated pleura. Most of the glands are located within the sterna but some are found around the outer edge (Figs. 5.16 and 5.17A). They are also located in the basipodites and to a lesser extent in the endopodites and exopodites of the pleopods. No glands were detected in the tail fan appendages, with the exception of several *A. franklinii* females which appeared to have small amounts of the round glands at the bases of the lateral uropodal rami.

When examined microscopically the individual glands are roughly circular with the characteristic "rosette" shape described in other Astacidea (Stephens, 1952; Aiken & Waddy, 1982).

Glair gland development was seen only in mature, reproductively active females and does not occur in mature nonreproducing females, mature males or immature individuals of either sex. The glands show cyclic development which closely follows the ovarian cycle of adult females (see Chapter 6).

Parastacoides: As in *Astacopsis*, the glair glands are creamy white and granular, and are found on the ventral surface of the abdomen. In *P.t. tasmanicus* (SP), they are found along the anterior edges of the abdominal sterna extending laterally into the associated pleura (Fig. 5.17B). A very few glands were seen in the pleopods of several females, but they are generally not present in any of the abdominal appendages (pleopods and uropods).

Glair gland development was seen only in mature, reproductively active females and was not observed in nonreproducing females, mature males or immature

Figure 5.16 Glair glands (G) in the abdominal sterna and pleopods of A. gouldi female (CPL 135 mm, March 1987). Note heavy setal fringes (S) along pleural edges and on last thoracic segment.



Figure 5.17 Glair gland development in:

A. *A. franklinii* (Eastern form)

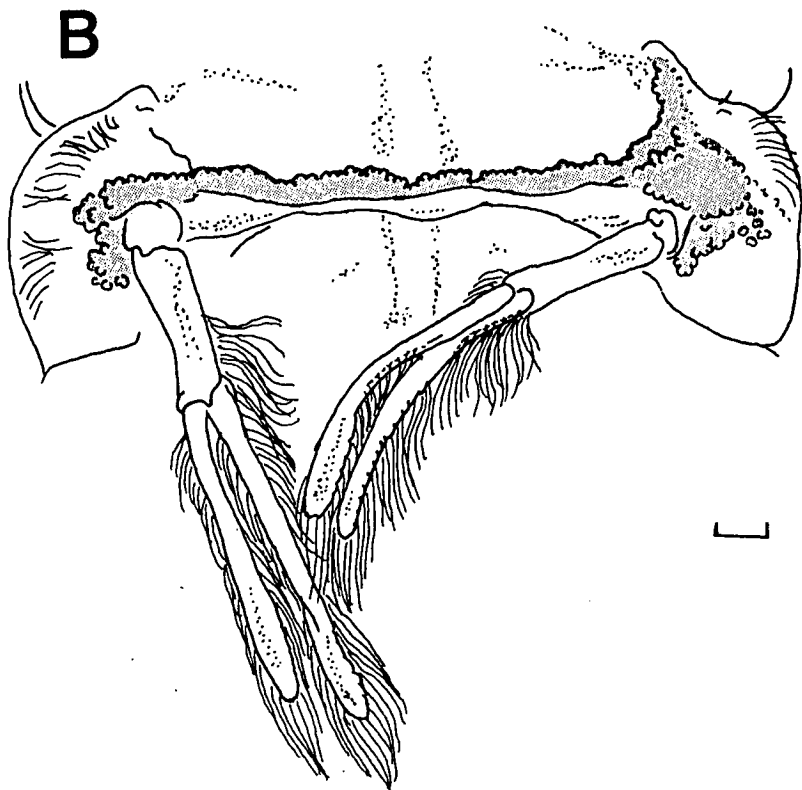
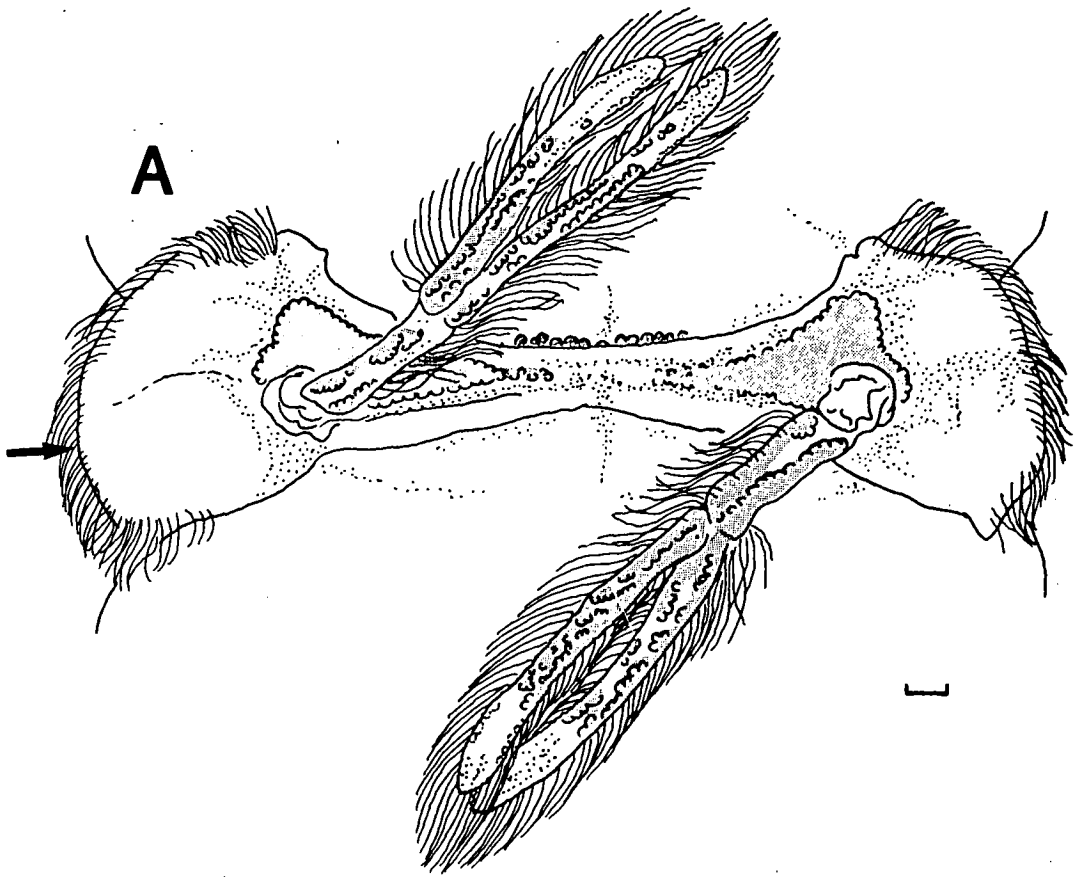
Female CPL 45.5 mm, Hobart Rivulet, 1.4.1987.

B. *P. t. tasmanicus* (SP)

Female CPL 32.0 mm, Harlequin Hill, 3.4.1987.

Ventral view of the second abdominal somite. Glair glands are shown as shaded areas, arrow indicates heavy setation along pleural edges in *Astacopsis*.

Scale bar = 1 mm



individuals of either sex. As in *Astacopsis*, the glands show cyclic development which closely follows the ovarian cycle of adult females (see Chapter 6).

B. Setation

Astacopsis: Setae first appear on the body and appendages of stage 2 juveniles (see Chapter 7). As male and female crayfish grow toward maturity, overall setation increases, reaching its peak at the onset of sexual maturity. The dimorphism of the setal armature in adult males and females is outlined below:

Gonopores: As shown in section 5.3.2 the gonopores of both sexes show increased setation at sexual maturity. This increase is particularly dramatic in females, where a dense ring of papose setae develops on the rim of the gonopore (Figs. 5.6-5.8). The function of this setal ring is unknown but it is present in all mature females prior to oviposition and may therefore play an important role in spawning.

Abdomen: Both sexes have papose setae fringing the pleura and tail fan appendages. The distribution of these setal fringes appears the same in both sexes but the number and length of the setae is markedly different. Females have longer and denser setae, making the ventral surfaces of their abdomens conspicuously setose, especially prior to oviposition when the setae are clean and in good condition following a pre-reproductive molt (Figs. 5.16 & 5.17A). In addition to this increased abdominal setation the last thoracic segments in females also display markedly increased setation. The most conspicuously setose of these are the lateral shield shaped epimeral plates which make up a part of the cephalothorax-abdomen hinge. The bular lobe and lateral processes of the median keel of the last thoracic sternum also bear a heavy setal cover. This increased setation combined with a characteristic abdomen flexion forms a water-tight egg chamber at the time of oviposition (see Chapter 7). In immature females, abdominal setation is identical to that of males and the denser cover of setae is gradually acquired as the females approach maturity.

Pleopods: Initially immature individuals of both sexes show identical setation of the pleopods. Their pleopods are fringed with plumose setae. As females approach maturity their pleopods gradually develop oosetae. Small numbers of oosetae are seen at first and peak density is not reached until sexual maturity. The smallest females showing initial development of ovisetae were CPL 119.5 mm for *A. gouldi*, CPL 36 mm for *A. franklinii* (Eastern form) and CPL 53.0 mm for *A. franklinii* (Western form). The ovisetae are filamentous (lacking setules) and longer

than the plumose setae (Fig. 5.18). These setae are for the attachment and carrying of extruded eggs and appear to be closely associated with glair glands present in the pleopod. Oosetae showed greatest density on the medial margin of the basipodite, lateral and medial margins of the proximal half of the endopodite and to a lesser extent on the lateral and medial margins of the proximal half of the exopodite (Fig. 5.19A&B).

Parastacoides: Setae first appear on the body and appendages of stage 2 juveniles (see Chapter 7). Setation increases gradually as males and females grow toward maturity. The dimorphism of the setal armature in adult individuals is outlined below:

Gonopores: As discussed in section 5.3.2 the gonopores of both sexes showed an increase in setation as the crayfish grew toward maturity. The peak density of the gonopore setae was reached at the attainment of sexual maturity. Adult females show greater setation of the gonopore than males but the setal cover is not as extensive as seen in *Astacopsis*.

Abdomen: As in *Astacopsis*, both sexes have setae fringing the abdominal pleura and tail fan appendages. The distribution, length and density of these setal fringes does not appear to be significantly different in the two sexes, however.

Pleopods: Initially immature individuals of both sexes show identical setation of the pleopods (fringes of plumose setae). As females approach maturity their pleopods gradually develop oosetae. The smallest *P.t.tasmanicus* (SP) female showing partial development of ovisetae was CPL 23.6 mm. The ovisetae are filamentous (lacking setules) and longer than the plumose setae (Fig. 5.18). Peak setal density is reached at the onset of sexual maturity. Oosetae are present on the basipodite and endopodite only and show the greatest density on the medial margin of the basipodite as well as on the lateral and medial margins of the proximal half of the endopodite (Fig. 5.20 A&B).

C. Tail fan

Astacopsis: The tail fan appendages of immature male and female individuals are initially identical in size and morphology. At sexual maturity these appendages become markedly different in the sexes. Mature females exhibit marked decalcification and elongation of the telson and the uropods (Fig. 5.21) while the tail fan of mature males remains small and well calcified. In the female, the


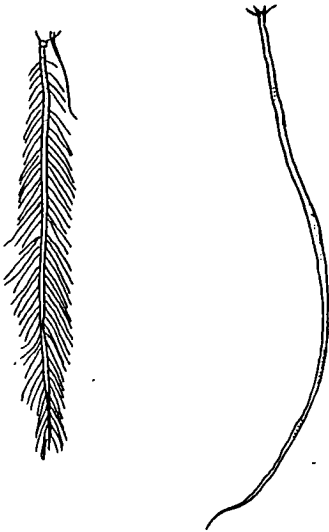
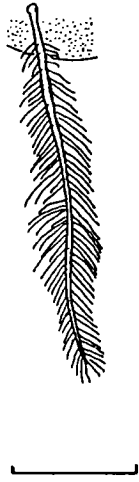

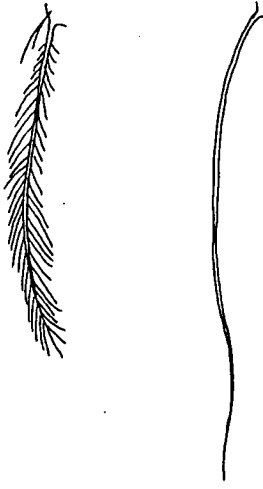

GONOPORE	PLEOPOD Plumose Ovisetae	ABDOMEN (Pleura)
	<p data-bbox="559 327 734 362"><u>Astacopsis</u></p> 	
	<p data-bbox="541 980 765 1015"><u>Parastacoides</u></p> 	

Figure 5.18 Major types of setae found on females of *Astacopsis* and *Parastacoides*.

Scale bar = 0.5 mm

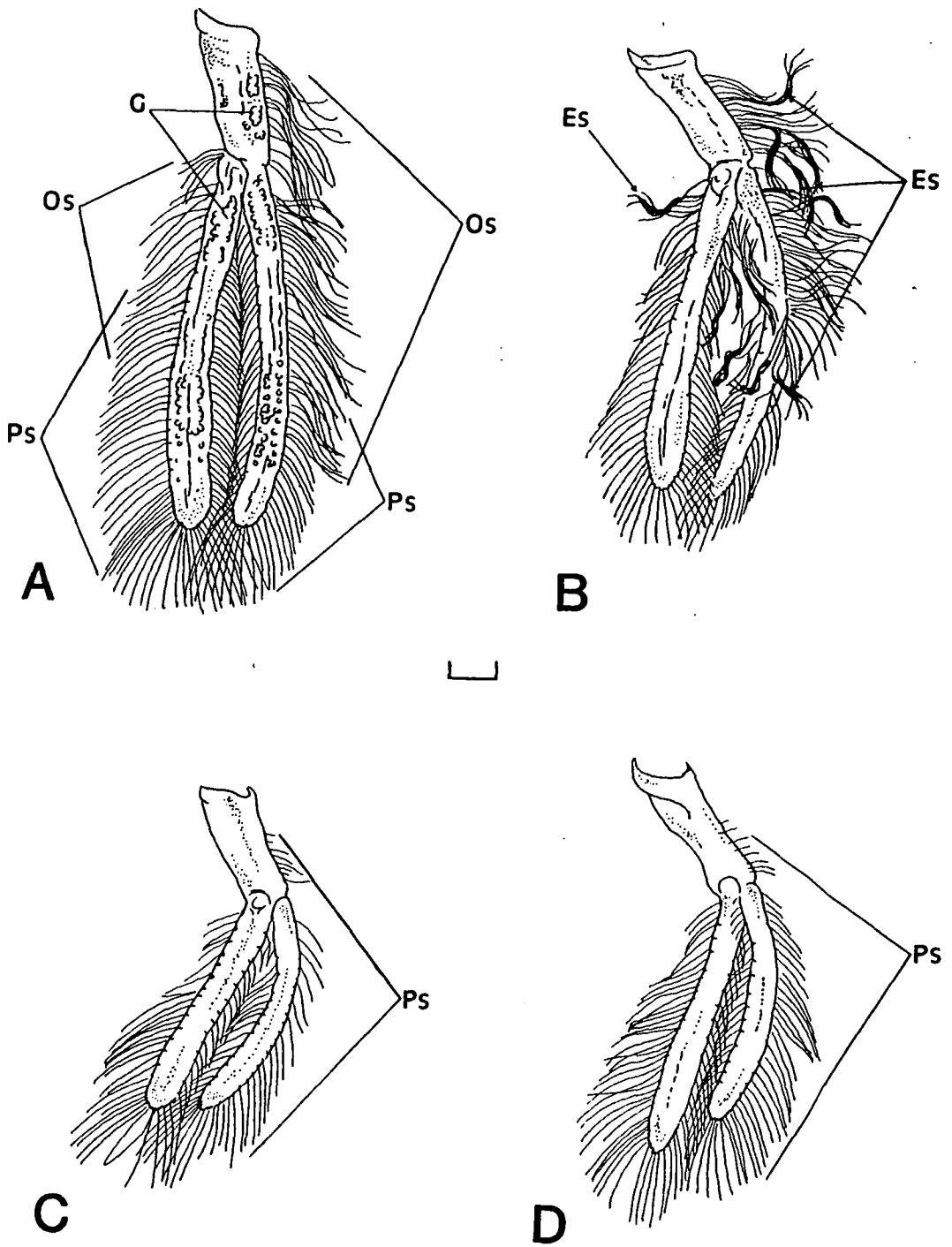


Figure 5.19 Second left pleopod of female *A. franklinii* (Eastern form).

A. Mature female(CPL 45.5 mm) just prior to oviposition.

B. Mature female(CPL 45.5 mm) 12 months after oviposition.

C. Immature female(CPL 38.5 mm).

D. Mature male(CPL 46.0 mm).

Abbreviations: PS: plumose setae; OS: oosetae; G: glair glands; ES: egg stalks.

Scale bar = 1 mm

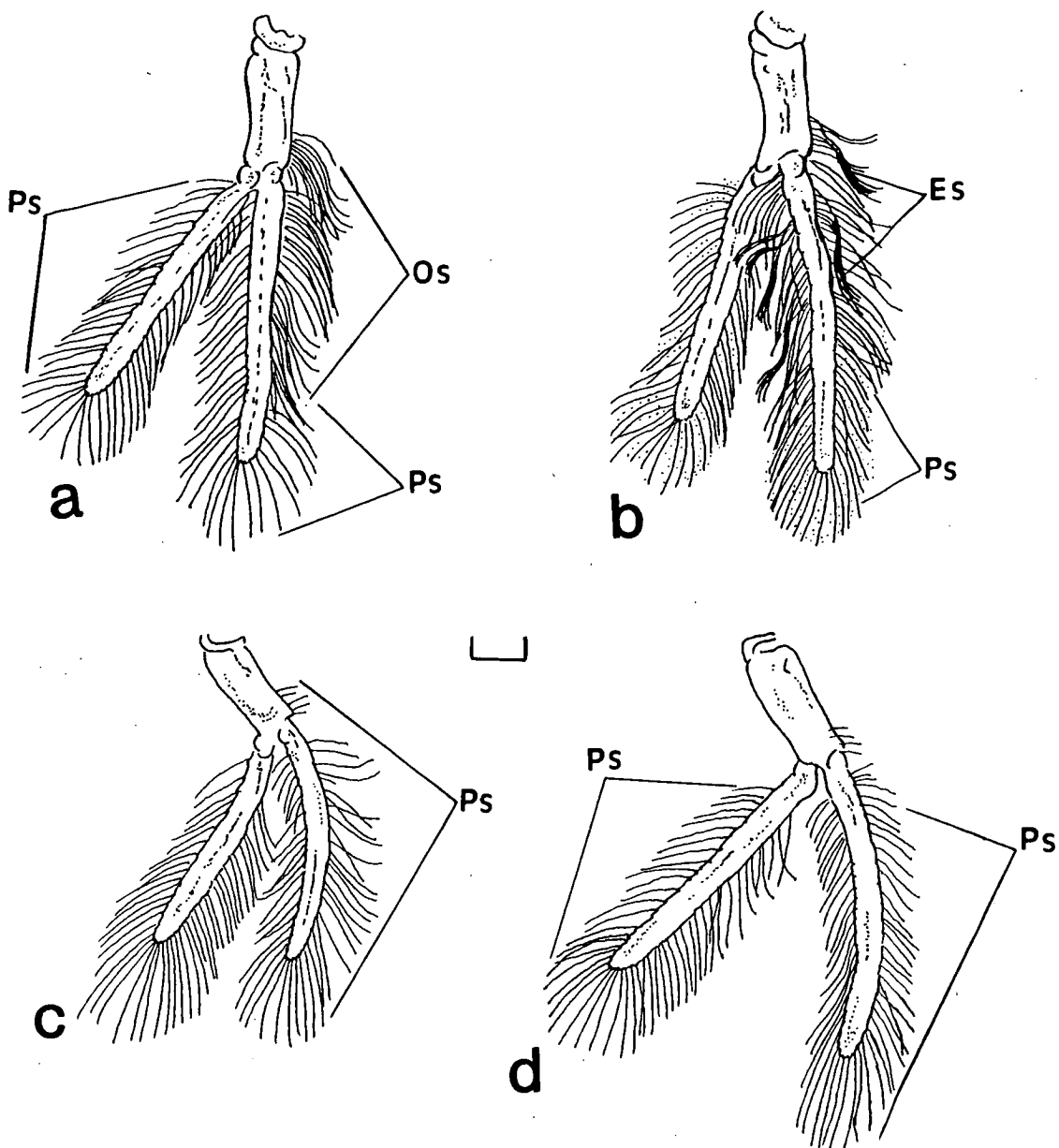


Figure 5.20 Second left pleopod of female *P. t. tasmanicus* (SP).

a. Mature female (CPL 30.0 mm) just prior to oviposition.

b. Mature female (CPL 30.5 mm) 12 months after oviposition.

c. Immature female (CPL 27 mm).

d. Mature male (CPL 31.3 mm).

Abbreviations: PS: plumose setae; OS: oosetae; G: glair glands; ES: egg stalks.

Scale bar = 1 mm

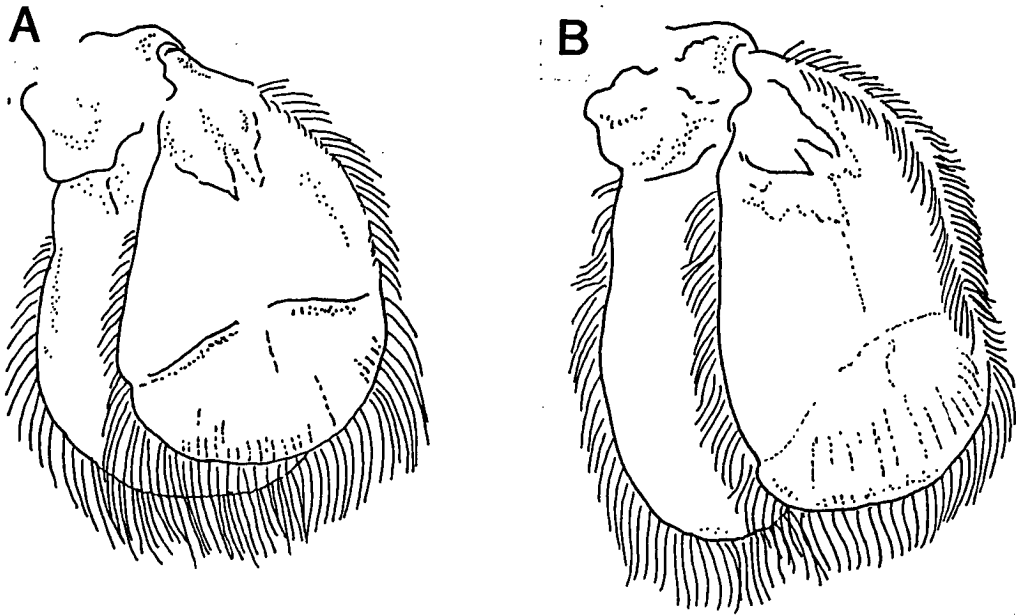


Figure 5.21 Left outer and inner uropodal rami of female *A. franklinii* (Eastern form).

A. Immature female (CPL 40.3 mm).

B. Mature female (CPL 40.0 mm).

Note increased setation on lateral edges and overall elongation of uropodal rami.

decalcification occurs mainly on the distal halves of the uropods and to a lesser extent on the extreme tip of the telson. This gives the female tail fan an overall membranous appearance. The decalcification and elongation occurs gradually in females approaching maturity but is marked at the onset and is therefore a good indicator of sexual maturity in *Astacopsis* (Figs. 5.22 and 5.23). Mean uropod length to carapace length ratios were found to be significantly different between mature males and females (*A. gouldi*: $t = 11.24$, $df = 26$, $p < 0.0001$; *A. franklinii* Eastern form: $t = 9.77$, $df = 32$, $p < 0.0001$; *A. franklinii* Western form: $t = 7.19$, $df = 18$, $p < 0.0001$). The acquisition of this character is a prerequisite for successful oviposition, as all ovigerous females examined exhibited the membranous tail fan.

Parastacoides: The tail fan appendages of male and female *Parastacoides* do not exhibit sexual dimorphism as in *Astacopsis*. The uropods are calcified in both males and females of all sizes. The uropod to carapace ratios were not significantly different between mature males and females ($t = 1.75$, $df = 41$, $p < 0.087$) and there appear to be no significant changes associated with the onset of sexual maturity (Fig. 5.24).

D. Abdomen

Astacopsis: Initially the abdomens of immature males and females are identical. As they approach maturity the females' abdominal terga become broader and the pleura deepen (Figs. 5.25A, 5.26A and 5.27A). This becomes most conspicuous at the onset of maturity when the abdomens of females are noticeably broader giving them a narrow waisted appearance. Mean abdomen width to carapace length ratios were found to be significantly different between mature males and females (*A. gouldi*: $t = 9.38$, $df = 43$, $p < 0.0001$; *A. franklinii* Eastern form: $t = 9.16$, $df = 39$, $p < 0.0001$; *A. franklinii* Western form: $t = 8.21$, $df = 43$, $p < 0.0001$).

The abdomen length also exhibits sexual dimorphism. There was a less obvious but significant difference in abdominal length between mature male and female *Astacopsis*. In immature and mature males abdomen length varies directly with carapace length while in females it varies directly with carapace length initially and then grows at faster rate from the onset of maturity (Figs. 5.25B, 5.26B and 5.27B). When the mean abdomen to carapace length ratios of mature males and females were compared there was a significant difference between the sexes (*A.*

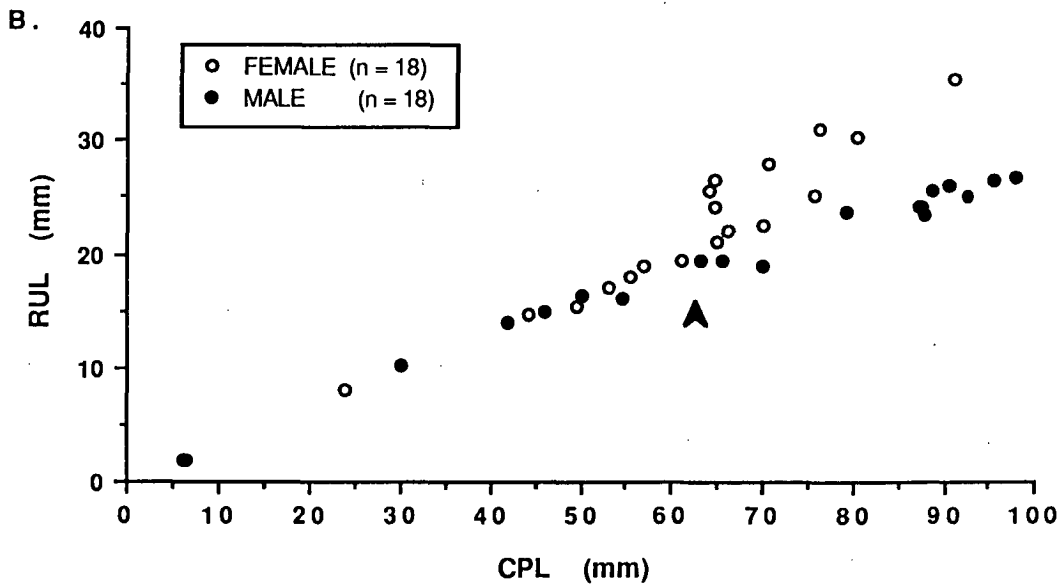
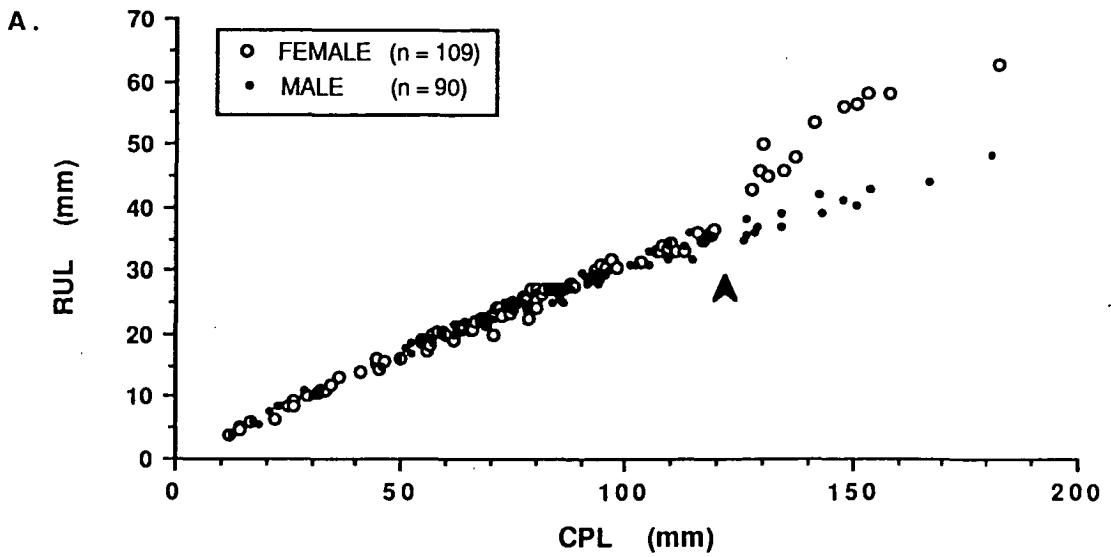


Figure 5.22 The relationship between the right uropod length and carapace length in males and females of:

A. *A. gouldi*

B. *A. franklinii* (Western form)

Arrow indicates size of smallest reproductive female.

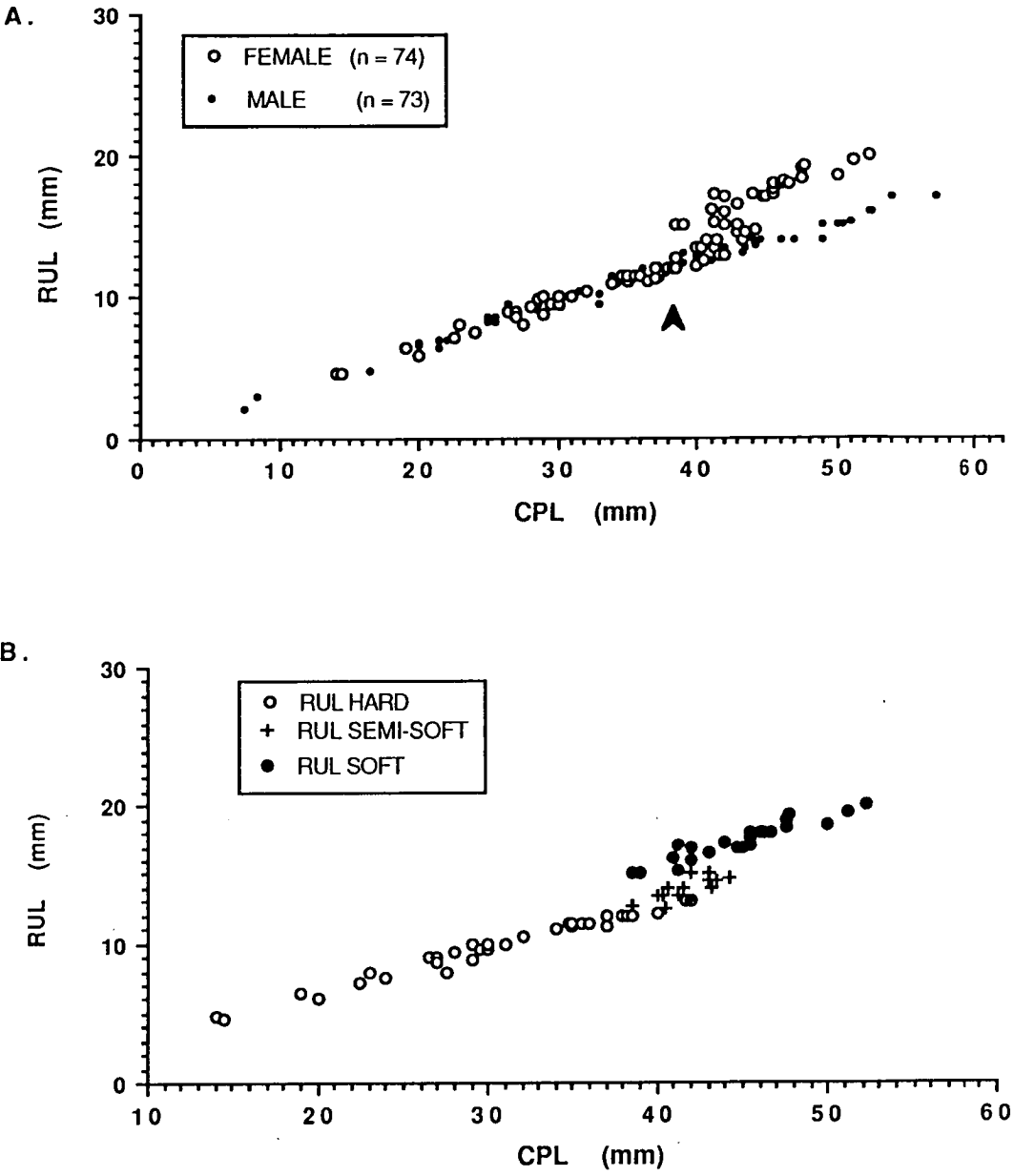


Figure 5.23

A. The relationship between the right uropod length and carapace length in males and females of *A. franklinii* (Eastern form).

B. The relationship between the right uropod length and carapace length in female *A. franklinii* (Eastern form) showing degree of calcification of uropods.

Arrow indicates size of smallest reproductive female.

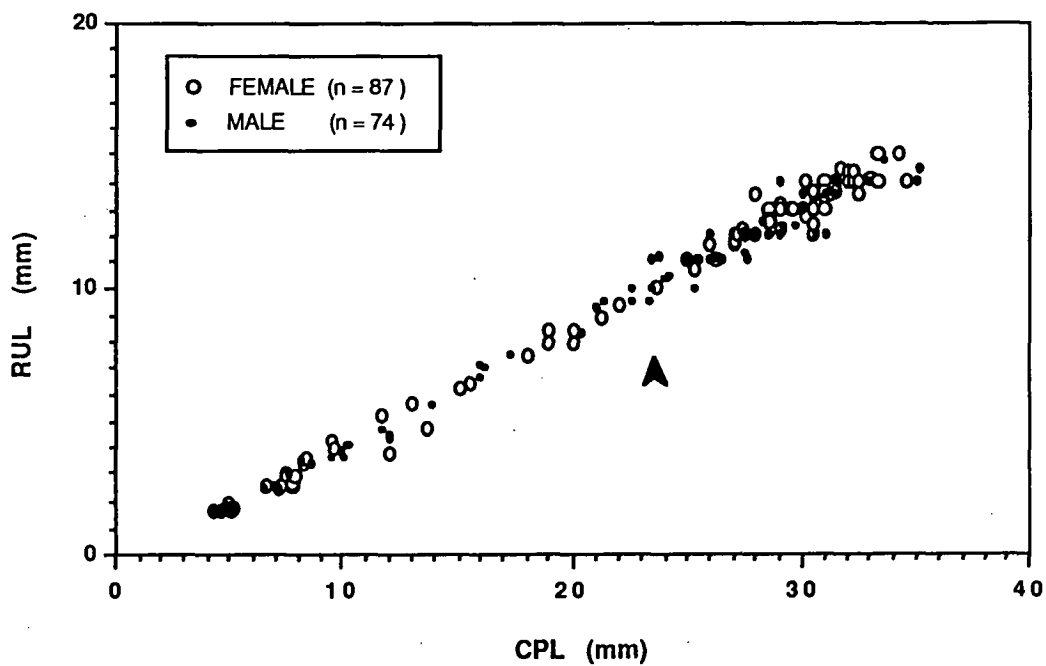


Figure 5.24. The relationship between the right uropod length and carapace length in female and male *Parastacoides t. tasmanicus* (SP). Arrow indicates size of smallest reproductive female.

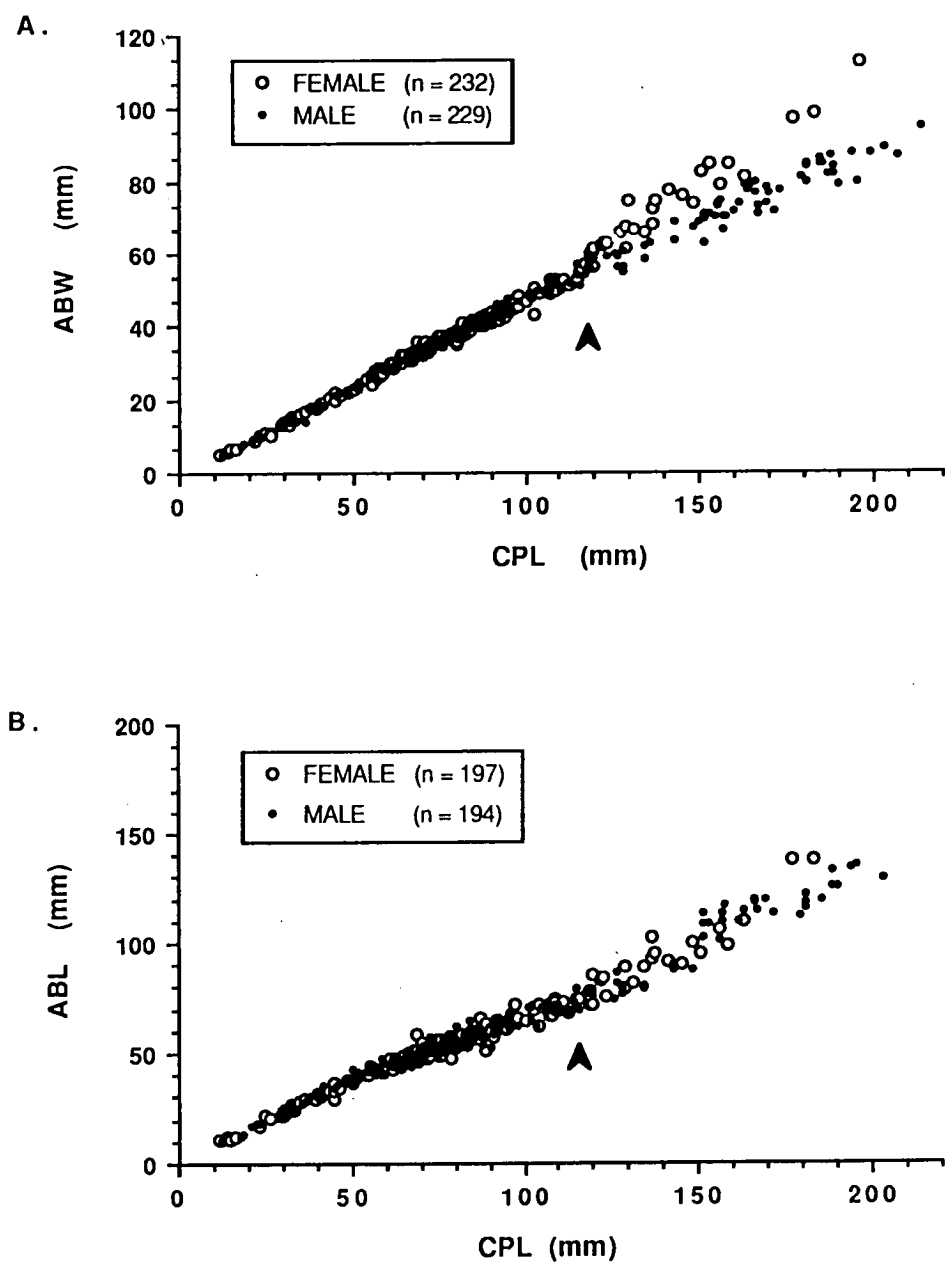


Figure 5.25 Abdominal growth in male and female *A. Gouldi*:

A. The relationship between the width of the second abdominal somite and carapace length.

B. The relationship between abdominal length (somites 1 to 5) and carapace length.

Arrow indicates size of smallest reproductive female.

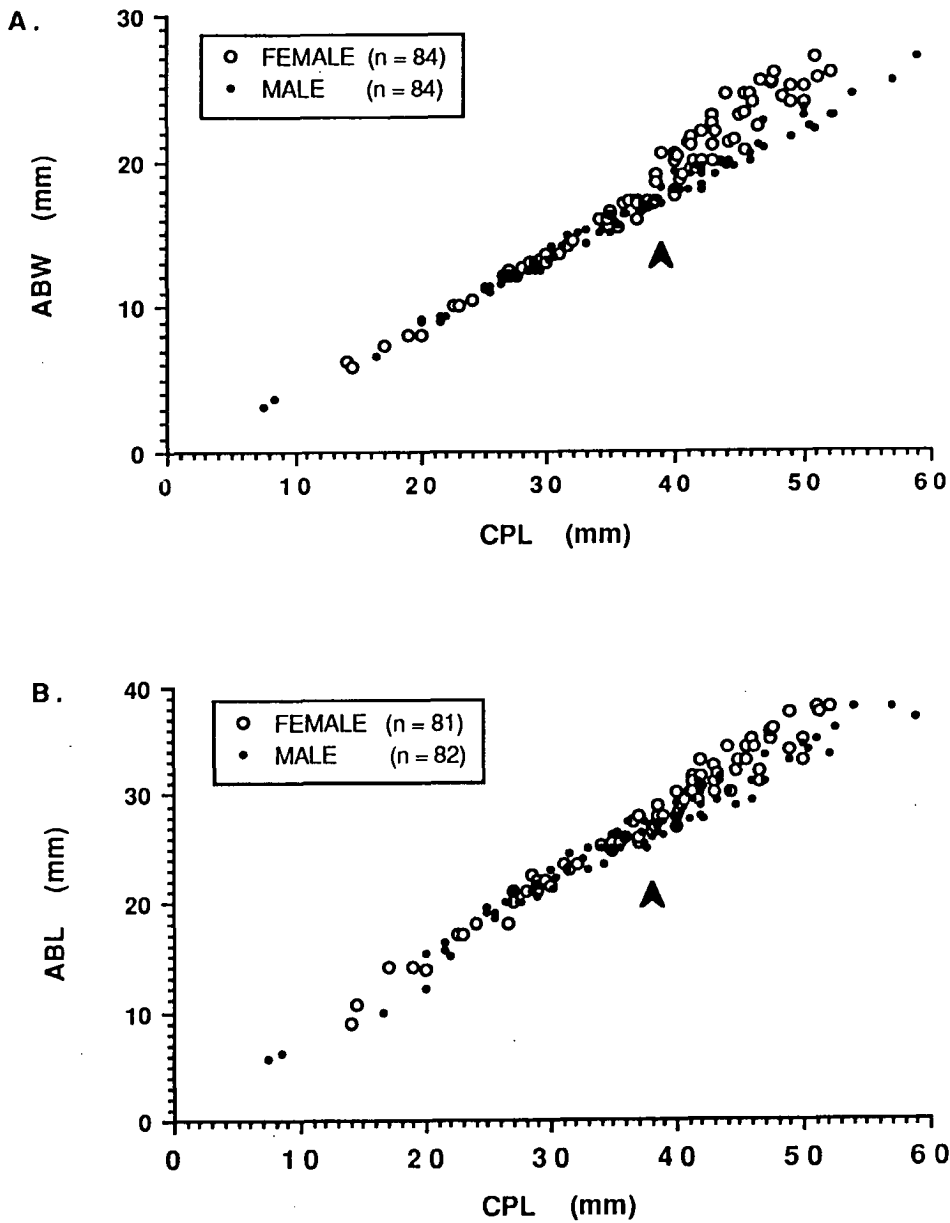


Figure 5.26 Abdominal growth in male and female *A. franklinii* (Eastern form):

A. The relationship between the width of the second abdominal somite and carapace length.

B. The relationship between abdominal length (somites 1 to 5) and carapace length.

Arrow indicates size of smallest reproductive female.

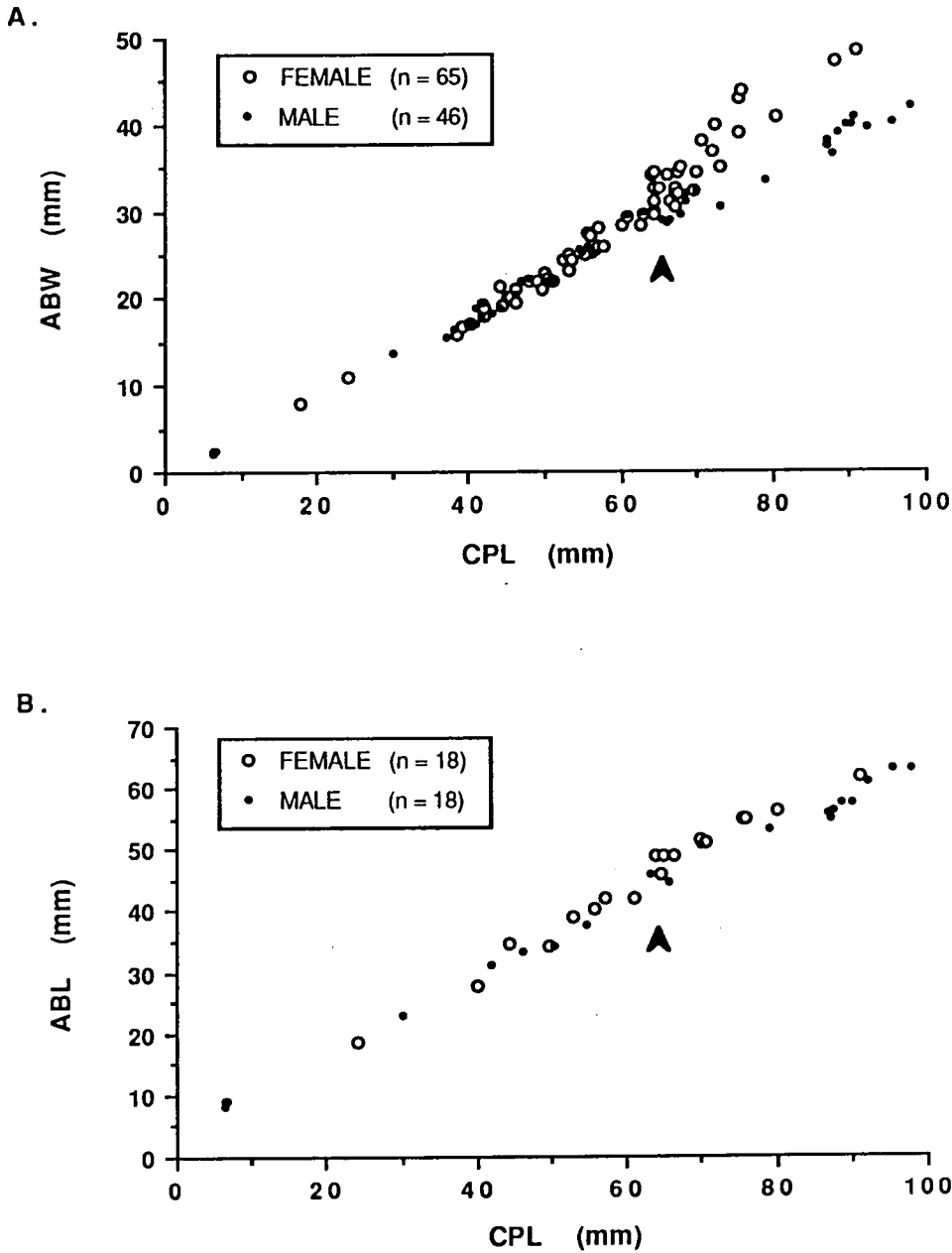


Figure 5.27 Abdominal growth in male and female *A. franklinii* (Western form):

A. The relationship between the width of the second abdominal somite and carapace length.

B. The relationship between abdominal length (somites 1 to 5) and carapace length.

Arrow indicates size of smallest reproductive female.

gouldi: $t = 4.42$, $df = 37$, $p < 0.0001$; *A. franklinii* Eastern form: $t = 5.43$, $df = 36$, $p < 0.0001$; *A. franklinii* Western form: $t = 5.22$, $df = 18$, $p < 0.0001$).

Parastacoides: The abdomens of male and female *Parastacoides* exhibit limited sexual dimorphism. Mature females have broader abdomens than males but the difference is less pronounced than in *Astacopsis* (Fig. 5.28A). When the mean abdomen width to carapace length ratios of mature males and females were compared, they were found to be significantly different ($t = 4.44$, $df = 44$, $p < 0.0001$).

The abdomen length does not exhibit sexual dimorphism (Fig. 5.28B). When the mean abdomen length to carapace length ratios of mature males and females were compared, there was no significant difference found between the sexes ($t = 1.65$, $df = 39$, $p < 0.10$).

E. Cephalothorax.

Astacopsis: The cephalothorax (carapace) of *Astacopsis* exhibits no obvious sexual dimorphism. When the mean carapace width to carapace length ratios of mature males and females were compared, no significant difference was found between the sexes (*A. gouldi*: $t = 1.89$, $df = 39$, $p < 0.066$; *A. franklinii* Eastern form: $t = 1.07$, $df = 39$, $p < 0.291$; *A. franklinii* Western form: $t = 4.23$, $df = 19$, $p < 0.677$). Cephalothorax width varies directly with carapace length and there appears to be no significant change associated with the onset of sexual maturity in either sex (Figs. 5.29 and 5.30A).

Parastacoides: No major differences were found in cephalothorax morphology of male and female *Parastacoides*. Cephalothorax width varies directly with carapace length and there appears to be no significant change associated with the onset of sexual maturity in either sex (Fig. 5.30B). When the mean carapace width to carapace length ratios of mature males and females were compared there was no significant difference between the sexes ($t = 0.248$, $df = 39$, $p < 0.806$).

F. Chelae.

Astacopsis: The chelae of *Astacopsis* display sexual dimorphism in mature animals. The chelae of immature male and female individuals are initially identical in size and morphology. Marked differences in chelae are not evident even after males first reach sexual maturity. As males grow larger, however, their chelae become conspicuously larger than those of same sized females (Figures 5.31 and 5.32A).

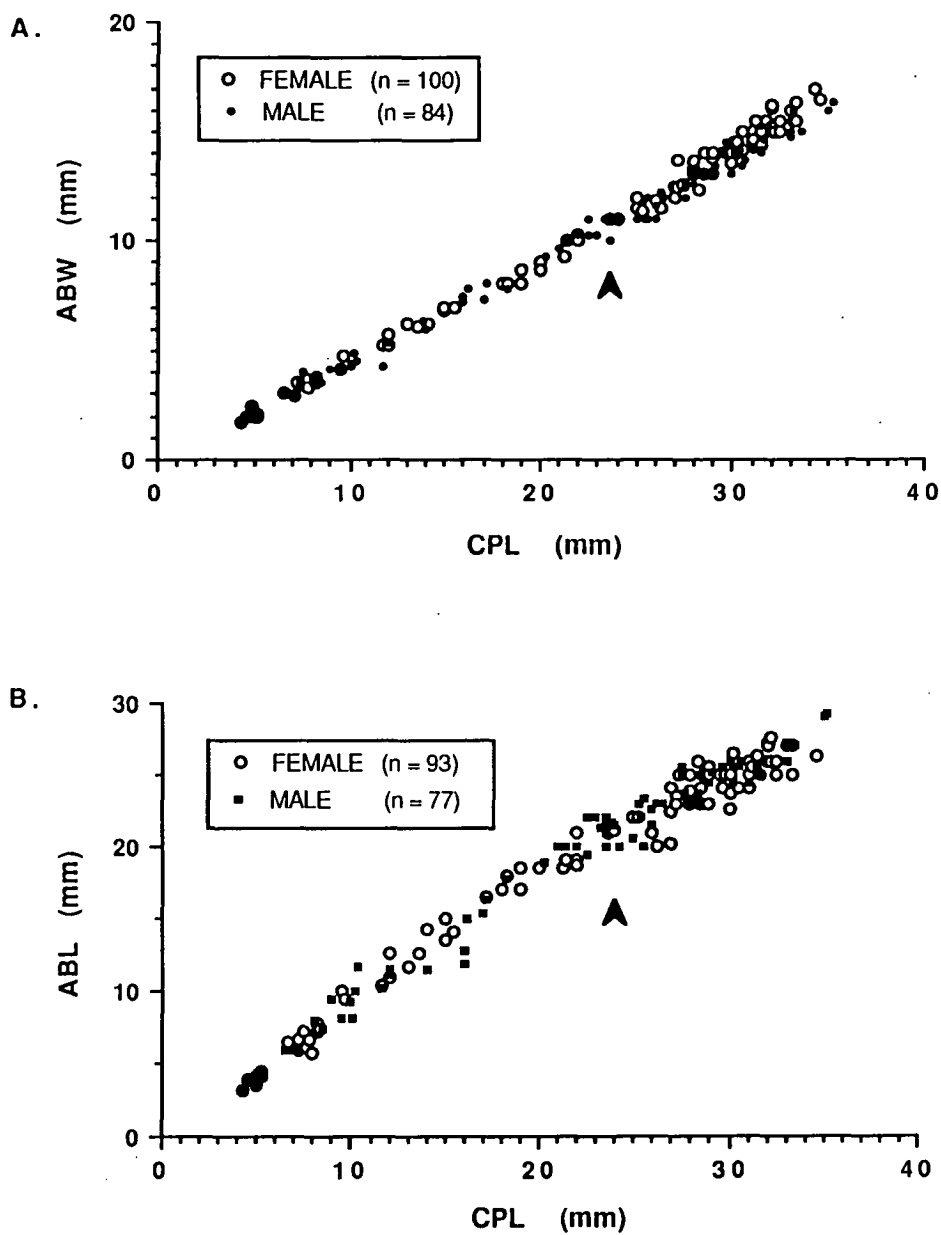


Figure 5.28 Abdominal growth in male and female *P. t. tasmanicus* (SP):

A. The relationship between the width of the second abdominal somite and carapace length.

B. The relationship between abdominal length (somites 1 to 5) and carapace length.

Arrow indicates size of smallest reproductive female.

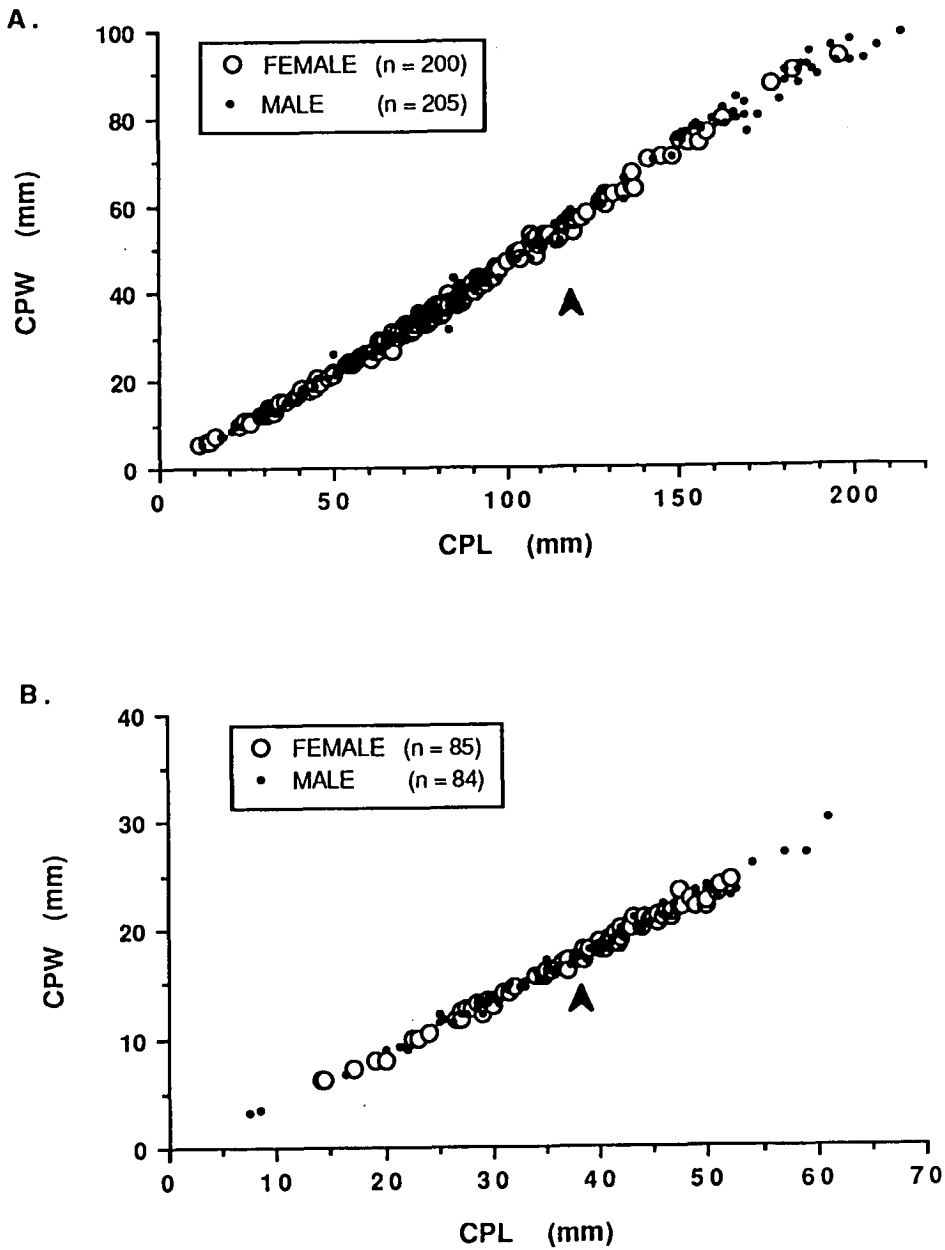


Figure 5.29 The relationship between carapace length and carapace width in males and females of:

A. *A. gouldi*

B. *A. franklinii* (Eastern form)

Arrow indicates size of smallest reproductive female.

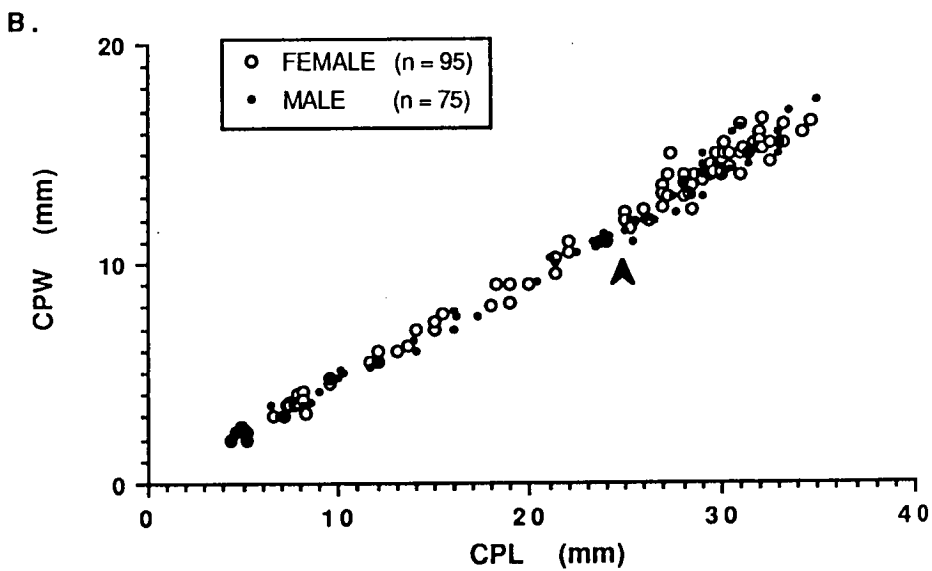
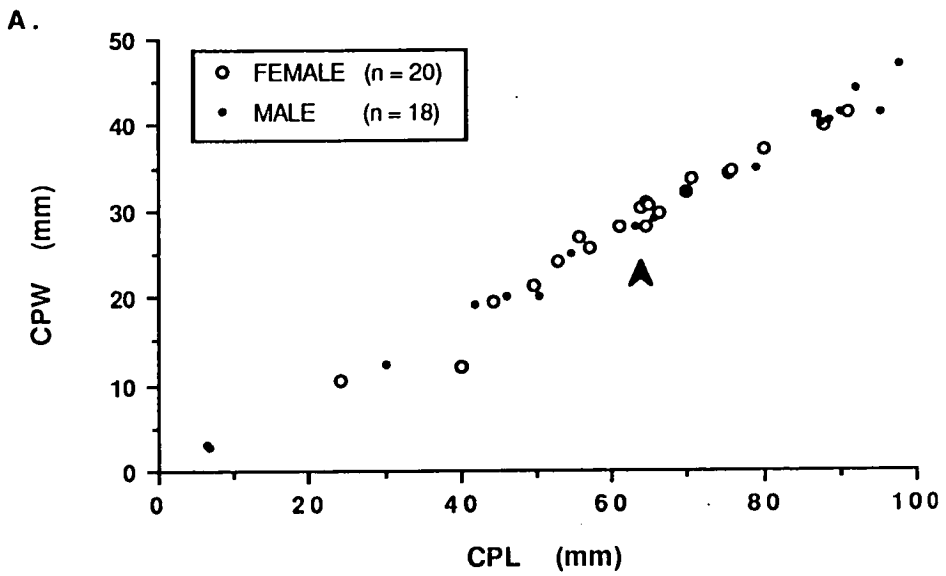


Figure 5.30 The relationship between carapace length and carapace width in males and females of:

A. *A. franklinii* (Western form)

B. *P. t. tasmanicus* (SP)

Arrow indicates size of smallest reproductive female.

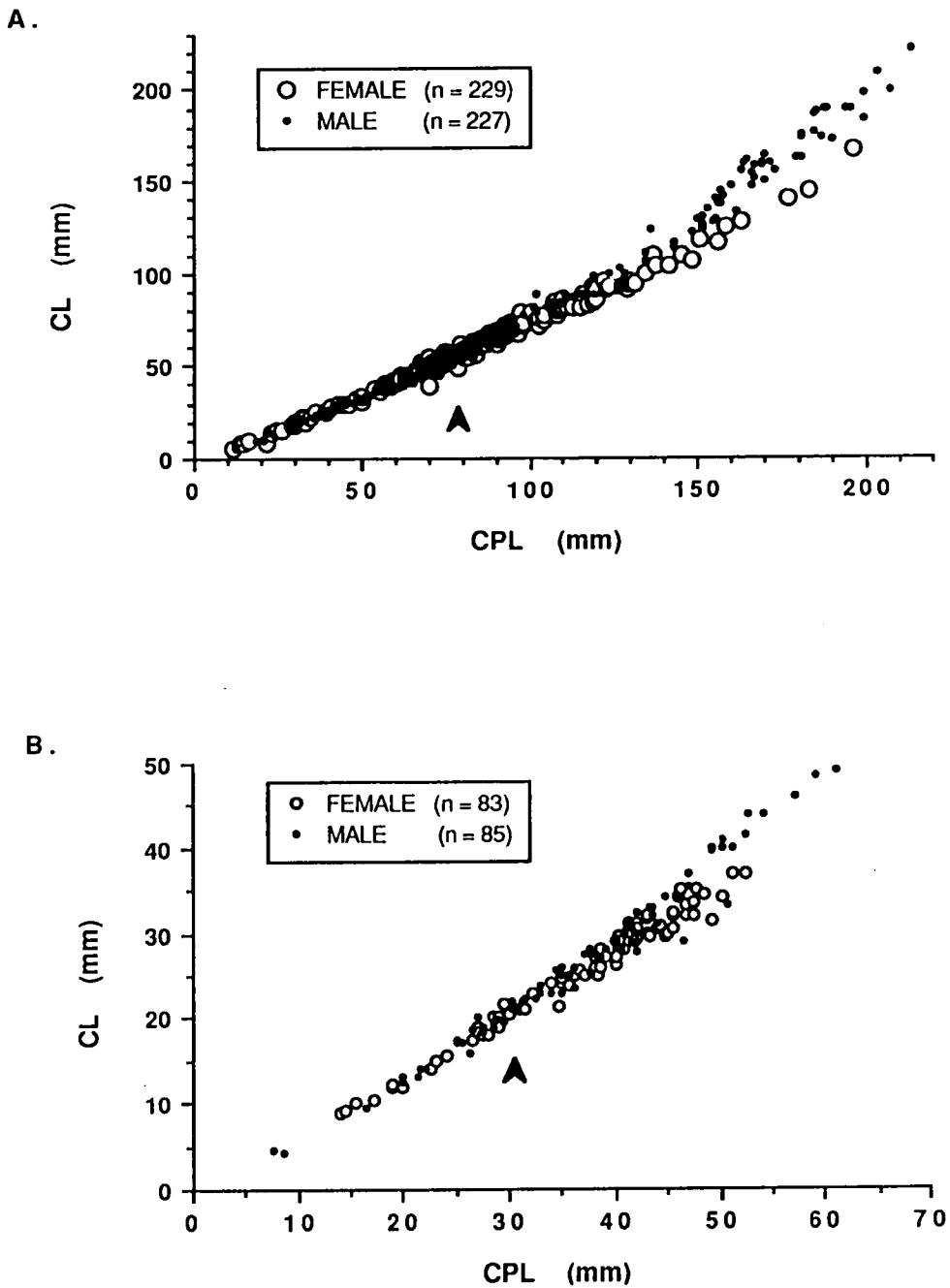


Figure 5.31 The relationship between carapace length and chela length in males and females of:

A. *A. gouldi*

B. *A. franklinii* (Eastern form)

Arrow indicates size of smallest reproductive female.

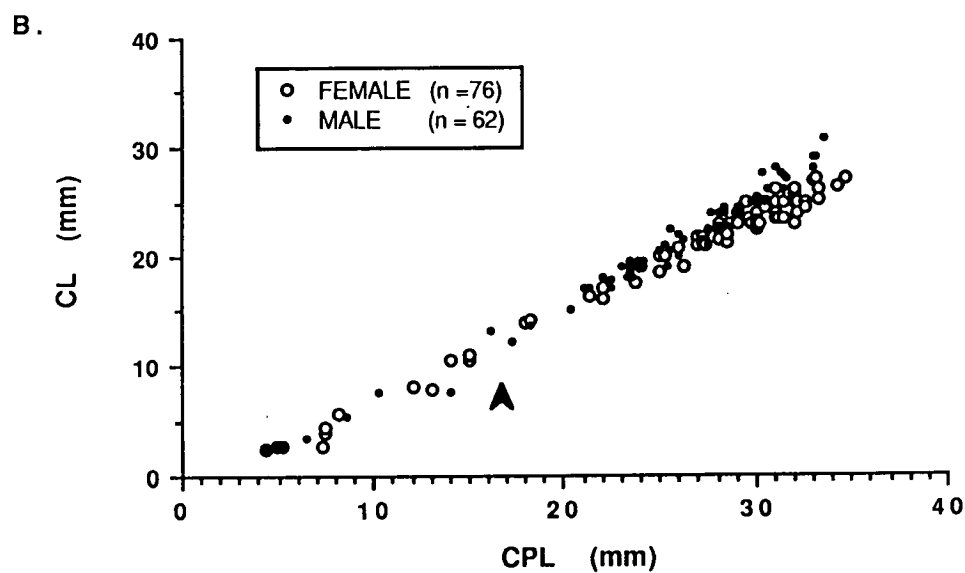
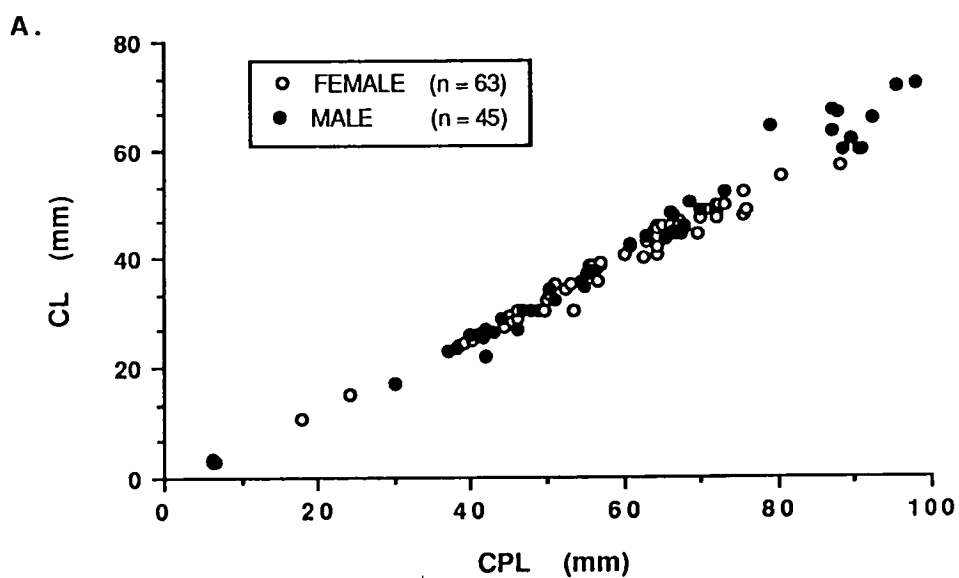


Figure 5.32 The relationship between carapace length and chela length in males and females of:

A. *A. franklinii* (Western form)

B. *P. t. tasmanicus* (SP)

Arrow indicates size of smallest reproductive female.

When the mean chela length to carapace length ratios of mature males and females were compared there was a highly significant difference found between the sexes (*A. gouldi*: $t = 4.55$, $df = 42$, $p < 0.0001$; *A. franklinii* Eastern form: $t = 4.97$, $df = 36$, $p < 0.0001$; *A. franklinii* Western form: $t = 2.19$, $df = 42$, $p < 0.034$). The chelipeds of males are not only larger but also more robust and the tubercles on the cutting edges are prominently raised. This allometric growth is most marked in very large specimens, and in *A. gouldi* the chelae can eventually become larger than the carapace. For example, the largest chela examined measured 222.0 mm and belonged to a male of 214 mm carapace length. Consequently, *A. gouldi* has the largest chela per carapace length of the three *Astacopsis* examined. CL/CPL ratios for mature crayfish of the three species/forms were as follows:

<i>A. gouldi</i> males.....	mean = 0.83 (s.d. = 0.08)
<i>A. gouldi</i> females.....	mean = 0.75 (s.d. = 0.03)
<i>A. franklinii</i> Eastern form males.....	mean = 0.77 (s.d. = 0.06)
<i>A. franklinii</i> Eastern form females.....	mean = 0.70 (s.d. = 0.03)
<i>A. franklinii</i> Western form males.....	mean = 0.71 (s.d. = 0.08)
<i>A. franklinii</i> Western form females.....	mean = 0.67 (s.d. = 0.02)

Parastacoides: The chelae of *P. t. tasmanicus* (SP) show marked sexual dimorphism in mature animals. As in *Astacopsis* there is no difference in chelae of immature males and females and the increase in size of male chelae takes place gradually, following the onset of maturity (Fig. 5.32B). When the mean chela length to carapace length ratios of mature males and females were compared there was a significant difference found between the sexes ($t = 9.33$, $df = 47$, $p < 0.0001$). The chelipeds of males are not only larger but also more robust with heavily calcified incurved fingers. The chela length does not exceed carapace length with the mean CL/CPL ratio being 0.87 (s.d. = .03) for mature males and 0.78 (s.d. = 0.03) for mature females.

G. Body Weight

Astacopsis: There was no significant difference between the body weights of male and female in *A. franklinii* Eastern form (Fig. 5.33 A). When the mean weights of mature male and females (CPL 44 -50) were compared there was no

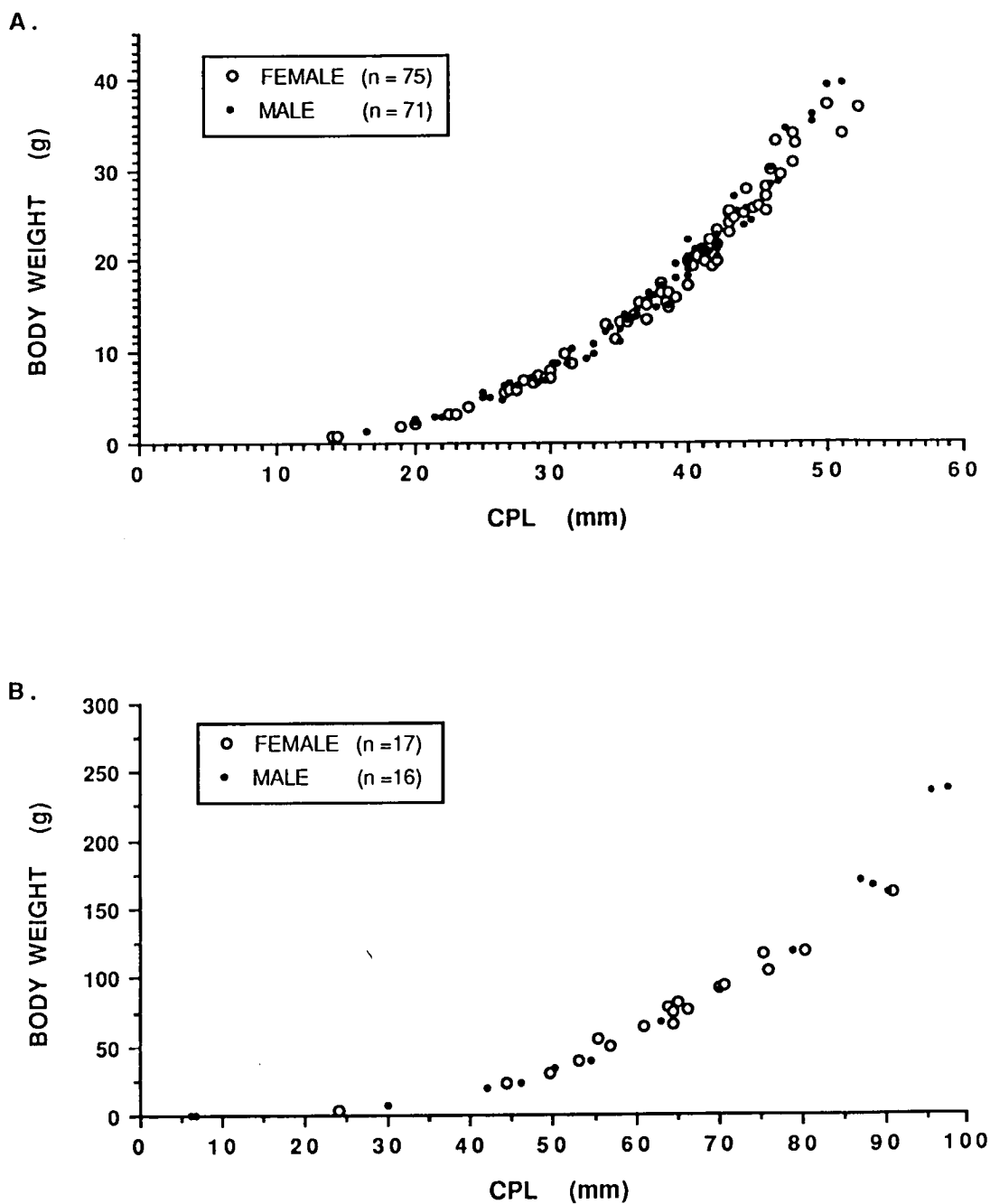


Figure 5.33 The relationship between carapace length and total body weight in males and females of:

A. *A. franklinii* (Eastern form)

B. *A. franklinii* (Western form)

Arrow indicates size of smallest reproductive female.

significant difference found ($t = 0.625$, d.f. = 22, $p < .539$; Female mean wt. = 29.4, s.d = 3.7, Male mean wt. = 30.4, s.d.=2.9). A similar trend is seen in *A. gouldi* and *A. franklinii* Western form (Figs. 5.33B and 5.34A) although the samples were not large enough to compare statistically.

Parastacoides: *P. t. tasmanicus* (SP) showed a small but significant difference in the body weights of adult males and females (Figs. 5.34B). When the mean weights of mature males and females (CPL ≥ 30) were compared there was a significant difference found ($t = 2.40$, d.f. = 57, $p < 0.02$; Female mean wt. = 12.4 g, s.d = 1.9, Male mean wt. = 13.6 g, s.d.=1.8).

5.4 DISCUSSION

A. Anatomy and development of gonads

The position in the body cavity of the male and female reproductive organs of *Astacopsis* and *Parastacoides* is similar to that observed in other crayfishes and related Decapoda (Huxley, 1880; Word & Hobbs, 1958; Paterson, 1968; Lowe, 1971; Farmer, 1974a; Turvey, 1980; Aiken & Waddy 1980).

The ovaries of *Astacopsis* and *Parastacoides* are similar in their basic structure (paired lobes connected by a single commissure). In other Parastacidae, similar gross anatomy has been observed in *Euastacus spinifer* (Turvey, 1980) but *Cherax destructor* and *C. tenuimanus* differ by having anterior extensions of the ovaries which form additional small lobes lateral to the cardiac stomach (Morrissey, 1970; Johnson, 1979). The purpose of these additional anterior lobes is unclear but it may be related to the overall higher reproductive activity documented for *Cherax* (Johnson, 1979). Further comparative studies are needed to establish whether the basic structure characteristic of *Astacopsis* and *Parastacoides* ovary is typical of other Parastacidae. This bilobed, roughly "H" shaped structure of the ovary is also typically seen in Nephropidae and Palinuridae (Yonge, 1937; Paterson, 1968; Farmer, 1974a; Phillips et. al., 1980). In contrast, the ovaries of the northern hemisphere Astacidae and the Cambaridae appear to be trilobed or "Y" shaped having the posterior region fused into a single lobe (Huxley, 1880; Lowe, 1971; Arrignon, 1981; Holdich & Reeve, 1988).

The testes of *Astacopsis* and *Parastacoides* are roughly H shaped and are

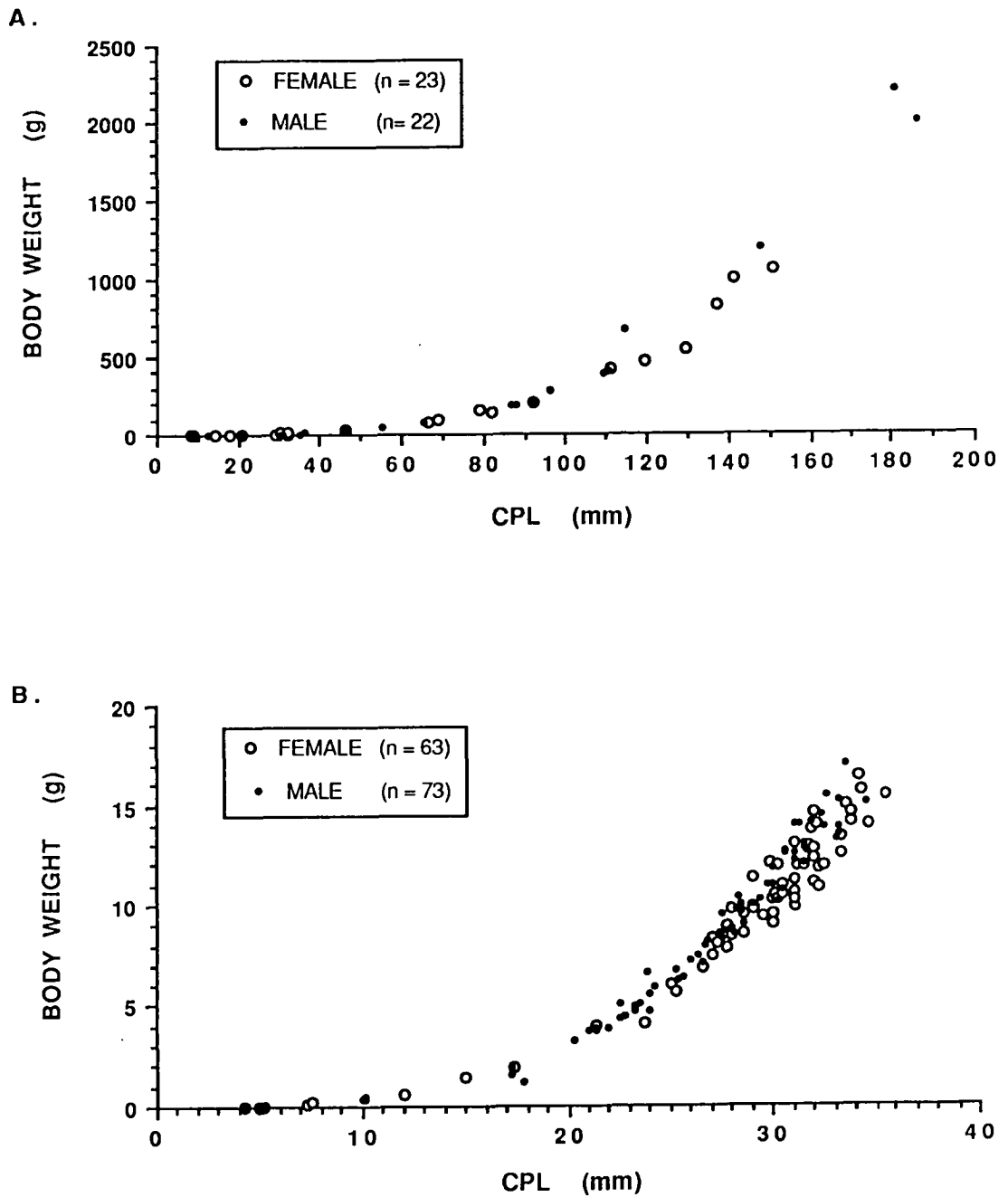


Figure 5.34 The relationship between carapace length and total body weight in males and females of:

A. *A. gouldi*

B. *P. t. tasmanicus* (SP)

Arrow indicates size of smallest reproductive female.

anatomically similar to those of other Parastacidae described to date: *Euastacus spinifer* (Turvey, 1980), *Cherax albidus* (Talbot and Beach, 1989) and *Cherax destructor* (Johnson, 1979). The testes and vas deferens of all four abovementioned genera differ slightly in their morphology, however. Additionally, interspecific variations were noted within *Astacopsis*, suggesting possible generic and perhaps specific differences in gonad morphology within the family Parastacidae. The parastacid male gonads appear to be most similar to those of palinurid lobsters, whose gonads are "H" shaped with a highly coiled vas deferens (Paterson, 1968; Aiken & Waddy, 1980). Nephropid lobsters also have "H" shaped testes but their vasa deferentia are not coiled (Farmer, 1974a; Aiken & Waddy, 1980). In contrast, the testes of the northern hemisphere Astacidae and the Cambaridae are trilobed or "Y" shaped, having the posterior region fused into a single lobe (Huxley, 1880; Word & Hobbs, 1958; Arrignon, 1981; Dudenhausen & Talbot, 1983). The vasa deferentia of these northern hemisphere crayfishes are coiled.

A histological comparative study of the testes of selected Astacidea (Hobbs & Hamr, in preparation) has shown that the acinar patterns as well as the life cycle of an acinus are different in Cambarids and Parastacids: Word and Hobbs (1958) showed that in the trilobed testis of *Cambarus*, the apical region of each lobe is capped by a band of budding acini containing spermatogonia. Beneath the cap is a broad zone in which spermatocytes are in the prophase stage of their first meiotic division, and the remainder of each lobe consists of a relatively thin layer of acini containing spermatids or spermatozoa. The base of each lobe and the Y-shaped stalk joining them contain the main efferent spermatic ducts, connective tissue and the degenerate or degenerating acini in which spermatozoa were produced just prior to and during the last breeding season. In the testis of *Parastacoides* (at a comparable stage), there is no evidence of zonation in activity either in the longitudinal lobes or the transverse bridge. The main efferent ducts are found roughly in the longer axis of each of the two longitudinal lobes, and radiating from them are the branching collecting tubules leading to the acini (most of which are either spent or contain spermatids and or spermatozoa). Acini in early formative stages are closely associated with those that are spent. Up and down the lengths and widths of the lobes and the transverse bridge, there is little if any difference in the variety of sperm production present. Thus, in any area of the testis, elements associated with the production of sperm of two breeding seasons lie adjacent to one another, and acini that have degenerated to

some degree are not abandoned and shunted to one area of the testis but are incorporated into the functional system already preparing for the next breeding season.

The three regions of the vas deferens described here are consistent with the descriptions of the vas deferens of *Cherax albidus* (Talbot and Beach, 1989), *Euastacus spinifer* (Turvey, 1980) and *Cherax destructor* (Johnson, 1979). The morphology of the parastacid vas deferens is most similar to the structure seen in the vas deferens of the palinurid lobster *Jasus lalandii* (Paterson, 1968). In the Astacidae and the Cambaridae, although loosely coiled, the vas deferens apparently does not show the three distinct regions, and in some species, varies little in diameter throughout its length (Huxley, 1880; Arrignon, 1981; Dudenhausen & Talbot, 1983).

The development of male and female gonads from immature to mature state in *Astacopsis* and *Parastacoides* is comparable to the scarce data available for other Astacidea (Lowe, 1961; Farmer, 1974a; Phillips et.al., 1980; Turvey, 1980).

B. Anatomy and development of genitalia

Although superficially simple genital structures, the parastacid gonopores show considerable complexity and variation among genera. This variation is especially prominent in the males, where the gonopores consist of raised genital papillae. Riek (1976) recognized this diversity in form and divided the Parastacidae into groups according to the structure of the male papillae. He separated *Astacopsis*, *Euastacus*, *Astacoides* and *Samastacus* as one group on the basis of a partial or complete sclerotized ring on the papilla. This ring, separated from the coxopodite by a membrane, is not found in the remaining members of the family, which include *Parastacoides*, placed in a sub-group with *Cherax*, *Paranephrops* and *Gramastacus* on the basis of papilla size. Morgan (1983 & 1986) examined the gonopores of *Euastacus* in his generic revision and stated that the male genital papilla of *Astacopsis* is more tubular than that of *Euastacus*. He also found variability in the presence of the cuticular partition between the papillar and arthrodial membranes within *Euastacus*. Such variability of the partition was not found in *Astacopsis*. Hobbs' study of *Astacoides* (1987) indicated some similarities between the papillae of *Astacopsis* and *Astacoides*.

This study has shown that detailed morphological studies of male papillae reveal

considerable complexity in structure. Major differences in morphology were observed between male *Astacopsis* and *Parastacoides*, including the opening mechanism of the gonopores. The female gonopores of the Parastacidae show greater similarity in structure but major differences occur in the amount and distribution of setae around the openings. In *Astacopsis* the setal cover around the gonopore is particularly heavy in mature females and, although its function is not clear, it appears to play an important role in egg extrusion. As setae are often associated with tegumental glands, it is possible that they apply secretions to extruding ova. Alternatively the setal rings may act to funnel the ova posteriorly in the direction of the brood chamber formed by the abdomen. The decalcification of the gonopore cover in mature females is presumably associated with the mechanics of egg extrusion. The calcified gonopore covers of immature females are tightly closed and cannot be opened, even forcibly, while decalcified covers of mature females can be easily pushed aside with a probe. Similar increased setation and/or decalcification has been noted and used as an indicator of sexual maturity in females of *Euastacus* (Turvey, 1980; Morgan, 1986) and *Engaeus* (Horwitz, 1988).

Further detailed studies of the genital structures of other Parastacidae are needed to reveal evolutionary trends and relationships within the family. As the gonopores change in structure during development and later according to breeding condition (some genera only), these changes will be pertinent to any future investigations or taxonomic revisions.

C. Secondary sexual characters/sexual dimorphism

Sexually mature females approaching the reproductive season in both *Astacopsis* and *Parastacoides* show marked development of glair glands on their abdomens. The concentration of the glands varies between the two genera, with *Astacopsis* showing a greater number of glands within the pleopods. Glair glands have not previously been described in any of the Parastacidae although their presence has been assumed by some authors (Mills, 1983). The distribution of glair glands in the two parastacids is comparable to that observed in *Homarus* (Aiken & Waddy, 1980) but differs from that of *Orconectes* and *Austropotamobius* by the absence of glands in the uropods (Stephens, 1952; Thomas & Ingle, 1987).

The decalcification and elongation of the tail fan appendages seen in mature *Astacopsis* females has also been documented in reproductive females of *Engaeus*.

Engaeid tail fan appendages are significantly longer in females and the mesal portions of their uropodal rami show decreased calcification (Horwitz, 1988). It is important that this dimorphic character is considered in future taxonomic revisions, as the degree of calcification of the tail fan has been used as a diagnostic character in previous classification schemes (Clark, 1936; Riek, 1969).

The oosetae of *Astacopsis* and *Parastacoides* were similar to those of other Parastacidae. The setae were filamentous and completely smooth, apparently lacking the apical setules seen in *Euastacus* and *Paranephrops* (Hopkins, 1967 - Fig. 2c; Turvey, 1980). Filamentous, apparently smooth oosetae are also present in *Cherax destructor* and *Cherax albidus* (Woodland, 1967; Johnson, 1979). Personal observations of the oosetae of *Engaeus* show that their form is highly variable, ranging from long and slightly plumose in some species to almost entirely plumose in others. Similarly, the ovigerous setae of the North American genus *Orconectes* appear to be fully plumose (Andrews, 1907-Plate VII). The oosetae of the European crayfish *Austropotamobius* are long and grooved proximally with apical setules (Thomas, 1970) as are those of the lobster *Homarus*. The oosetae of *Panulirus* and *Jasus* are described as non plumose, ie: lacking setules (Aiken & Waddy, 1980). Farmer (1974b) found the oosetae of the European lobster *Nephrops* were long and gently tapering, with slightly plumose tips. He noted that the apical setules, although obvious in recently moulted individuals, are eventually lost, probably by abrasion. Yonge (1937) regards oosetae as specialized plumose setae which have elongated and lost their lateral branches. He also states that the ducts of glair glands pass into the interior of oosetae and their secretion is discharged through the sides of these setae. This, in his view, explains the attachment of eggs exclusively to these setae. Further histological and scanning electron microscopy studies of oosetae and associated glair glands are needed to fully understand their function in the various Astacidean families.

Increased setation of the abdomen in mature females was seen in *Astacopsis* but not in *Parastacoides*. Similar increase in setation has been described in the European crayfish *Austropotamobius pallipes* (Thomas, 1970; Thomas & Ingle, 1987) and the marine lobster *Homarus vulgaris* (Yonge, 1937). The heavy setation, when combined with abdominal flexion, forms an apparently watertight egg chamber. The effectiveness of this brood chamber, formed by cupping of the abdomen, appears to be crucial in initial attachment of ova to the pleopods (see Chapter 6.).

Chela dimorphism is widespread in the Astacidea and has been documented in the Cambaridae (Weagle & Ozburn, 1970; Stein, 1976; Villalobos, 1983; Price & Payne, 1984; Hamr & Berrill, 1985;), Astacidae (Linguist & Lahti, 1983; Thomas & Ingle, 1987; Köksal, 1988), Nephropidae (Farmer, 1974b; Aiken & Waddy, 1980) and to a lesser extent in the Parastacidae (Ritchie, 1978; Sokol, 1988). The larger size of chelae in male crayfishes and lobsters has been associated with male dominance and competition during the mating season (Stein, 1976; Phillips et. al., 1980; Berrill & Arsenault, 1984). The dimorphism in the chelae of *Astacopsis* and *Parastacoides* was marked and the size difference between the sexes was more pronounced when compared to data available for *Orconectes* and *Cambarus* (Hamr, 1983).

Increased width of abdominal somites in females has been well documented in marine lobsters and northern hemisphere crayfishes (Yonge, 1937; Farmer, 1974b; Linguist & Lahti, 1983; Villalobos, 1983; Price & Payne, 1984; Thomas & Ingle, 1987; Aiken & Waddy, 1980 & 1987; Lowery, 1988). Several authors have suggested that this character is a reliable indicator of female maturity. Among the Parastacidae it has also been documented in reproductive females of *Engaeus* (Horwitz, 1988), *Cherax* (Sokol, 1988), *Astacoides* (Hobbs, 1987) and *Geocharax* (Ritchie, 1978). In contrast, Bocic et. al. (1988) have found no significant difference in the abdomen dimensions of male and female *Samastacus* in Chile. In addition to wider abdomens, female *Astacopsis* also had longer abdomens. Although significant, the difference was very small and cannot be easily detected when crayfish are examined superficially. Abdomen length has not been found to be dimorphic in other crayfishes (Linguist & Lahti, 1983; Bocic et. al., 1988; Lowery, 1988). The increased abdominal proportions may be an adaptation for carrying of larger broods and additionally may function to increase protection of eggs and young during the prolonged incubation. The latter would be especially important in the case of some Tasmanian Parastacidae which can carry broods for up to ten months.

Astacopsis and *Parastacoides* did not show dimorphism in carapace width. This is in agreement with the results obtained in comparable studies of carapace dimensions in *Geocharax* (Ritchie, 1978) and *Samastacus* (Bocic et. al., 1988).

Males of *Parastacoides* displayed a greater total weight than females but the trend was not significant in *Astacopsis*. The very small but significant difference in weight observed in *Parastacoides* was most probably due to the larger, more robust chelae of large mature males. It is quite likely that such dimorphism also occurs in

large *A. gouldi* because of the males' large, heavily calcified chela. Dimorphism with respect to weight has been demonstrated in several freshwater crayfish (Linguist & Lahti, 1983; Bocic et. al., 1988; Köksal, 1988) but several species also showed no difference in weight between the sexes (Price & Payne, 1984; van den Brink et. al., 1988)

In summary, *Astacopsis* shows sexual dimorphism by the presence in mature females of glair glands, heavier abdominal setation, elongation and decalcification of uropods, presence of oostetae on pleopods, broader and deeper abdominal pleura as well as greater total length of the abdomen. Sexually dimorphic characters of *Parastacoides* females are represented by glair glands, oostetae on pleopods and broader and deeper abdominal pleura. The secondary sexual characters observed in male *Parastacoides* are greater total weight and larger chelae, while in *Astacopsis* males the sole character is the considerably larger chelae.

Sexual dimorphism is developed to a greater degree in *Astacopsis* than in *Parastacoides*. This is especially apparent in females where the development of secondary sexual characters appears closely correlated with spawning and brooding mechanisms. The results therefore suggest that the eggs of *Astacopsis* may be subject to greater stress and therefore require greater protection. Indeed one would expect that *Astacopsis* would be more vulnerable to fish predation and mechanical stress in its swift water habitats, with their greatly fluctuating water levels. Attacks of blackfish (*Gadopsis* sp) on broods of berried *A. gouldi* are often reported by local fishermen (Lynch, 1967) and even the largest individuals are frequently observed to be swept away in flood waters over rapids and waterfalls. In *Parastacoides* the extensive burrows provide protection from predation and since the water fluctuations within them are gradual the main source of stress would be physiological rather than mechanical. Alternately the reproductive system and/or behavioral adaptations of *Parastacoides* may be more efficient and therefore fewer morphological adaptations are required for successful rearing of young. For example, the glair glands of *Parastacoides* may produce cement which attaches eggs more rapidly and efficiently, or the egg cases themselves may be less vulnerable to mechanical and physiological stress.

In terms of evolutionary significance the differences in reproductive anatomy and morphology between the Parastacidae and the Astacidae - Cambaridae imply that the Parastacidae split from the ancestral crayfish lineage very early on in Astacidean

evolution. This view supports the classification scheme proposed by Hobbs in his phylogeny of freshwater crayfish families (1974 & 1988). Furthermore the similarities in gonad anatomy and reproductive mechanisms in general between the Parastacidae and the Palinuridae suggest that the divergence may have occurred at an even earlier stage with a primitive decapod ancestor giving rise to three distinct lines: the Nephropidae, the Astacidae - Cambaridae and the Parastacidae.

CHAPTER 6 : REPRODUCTIVE CYCLE

6.1 INTRODUCTION

Little is known about the reproductive biology of Tasmanian Parastacidae and the main body of information available deals with the burrowing or "land" crayfishes. Suter (1977) estimated that the spawning season of *Engaeus cisternarius* extends from October to April. He found eggs hatched in February and described the larval development of this species in some detail. This corresponds with Horwitz's (1986) observations of various *Engaeus* spp. in the state (females with eggs and young from November to January). Horwitz et. al. (1985) also documented the presence of family groups within the burrows of *E. leptorhyncus*. Lake and Newcombe (1975), in their study of the ecology of *Parastacoides t. tasmanicus*, found that eggs were carried over winter from April to November and hatchlings remained attached to their mothers until February-March. They also found that only 40 % of eligible females carried eggs and suggested there was a low level of fertilization. Fradd (1979), in his study of the eco-physiology of *Parastacoides*, postulated that the reason for the low fertility was that the females bred only once every two years, and he based his suggestion on the annual variation in the composition of body tissues.

The reproductive biology of *Astacopsis*, the only predominantly riverine/lacustrine genus found in Tasmania, has not been studied to date. Information gathered from anglers and fisheries inspectors suggests "pairing" of *A. gouldi* occurs in winter and newly hatched young are attached to females in late spring. Forteath (1985), in his aquaculture feasibility study of *A. gouldi*, found that captive females carried eggs from May to November, with hatching occurring in late November - early December, and post larvae remaining attached until late January - early February.

Similarly, there is no life history information available for the crayfishes of the genus *Geocharax* in Tasmania.

Various aspects of the reproductive biology of other Parastacidae have been documented to date. The life history of the genus *Cherax* has received particular attention. Seasonal reproduction, fecundity and size at maturity in *C. destructor* have been well documented (Lewis, 1976; Johnson, 1979; Lake & Sokol, 1986; Sokol; 1988; Mills, 1983 & 1989). The life history of the closely related *C. albidus* has

been studied by Woodland (1967) while the reproduction of the West Australian Marron (*C. tenuimanus*) has also been researched in some detail (Shipway, 1951; Morrissy, 1970).

Turvey (1980) described the annual breeding cycle, size at maturity, fecundity and some aspects of spawning in *Euastacus spinifer* while Johnson (1974) provided a summary of the reproductive biology of the closely related *Euastacus armatus*.

The spawning seasons of *Paranephrops planifrons* in New Zealand and *Samastacus spinifrons* in Chile were estimated from the number and occurrence of ovigerous females (Hopkins, 1967A; Bocic *et. al.*, 1988).

Astacopsis and *Parastacoides* appear to have a prolonged breeding cycle characteristic of crayfishes living in cold water environments and low latitudes (Momot, 1984). Eggs and young appear to be carried for relatively long period of time as compared to species of mainland Australia living in warmer waters. The suggestion that females of *Parastacoides* may have a two year reproductive cycle needs further investigation and documentation in wild populations. The aim of this part of the study was therefore to document the reproductive cycles in field populations of *Astacopsis* and *Parastacoides* as well as to investigate various related aspects of their reproductive biology and correlate the results to previous findings in terms of the species' distributions and evolutionary relationships.

This chapter examines in detail the reproductive biology of crayfishes in the Tasmanian genera *Astacopsis* and *Parastacoides*. The seasonal breeding cycle, reproductive size and fecundity are documented. The reproductive strategies of the two genera are compared to each other as well as to other members of the Parastacidae. The differences and similarities between parastacid, astacid, cambarid and nephropid reproductive biology are discussed.

6.2 METHODS

Various aspects of the reproductive biology of *A. gouldi*, *A. franklinii* (Eastern form) and *P. t. tasmanicus* (SP) were studied in the field and the laboratory.

The seasonal reproductive cycle of each species was determined by examination of animals from monthly field samples as well as from observations of crayfish in the laboratory at seasonal water temperature and photoperiod. In each female captured,

the following reproductive characters were noted: occurrence and development of glair glands, calcification of uropods, setation and calcification of the gonopore as well as the development and condition of oosetae. During the mating season the presence of fresh or spent spermatophores on female sterna was carefully noted.

In females carrying broods, the eggs or young were counted and their development stage was noted (several eggs/young were removed for detailed study in the laboratory). Embryonic development was classified according to the sequence of embryonized stages (nauplius-protozoeca-mysis) described in previous studies (Huxley, 1880; Johnson, 1979). Each female was also visually inspected for ovarian development as ovaries could be clearly seen through the intersegmental membrane between the carapace and abdomen when the two were gently separated. The eggs were classified according to colour and size (large/brown, medium/brown, medium/yellow, small/white and not visible).

Mark recapture studies were used to document changes in reproductive condition of free-living individual crayfish. Field observations of reproductive activity were taken during regular sampling and the presence of mating pairs or family units within the same burrow or shelter were carefully recorded.

A portion of each catch was preserved for detailed laboratory examination. Samples ranged from ten to fifty animals depending on species and total monthly catch. Preserved individuals were weighed and checked for the presence of secondary sexual characters. The gonad of each animal was dissected out, placed on paper towelling to remove excess moisture and then weighed on an electronic balance. The condition and development stage of each gonad was also described. In males, the vasa deferentia were checked for the presence of spermatophores and their maximum diameter was recorded. In females the lengths and widths of ten representative ova were measured using an ocular micrometer. Their yolk content, shape and packing within the ovary were noted.

Because abdominal and ovarian eggs of both *Astacopsis* and *Parastacoides* were ovate in shape measurements of egg length and egg width were taken for each ovum. Average egg diameters were calculated as follows: $(\text{egg length} + \text{egg width} / 2)$.

A number of ovigerous females of each of the three species were transferred to the laboratory where egg development, larval growth and duration of each stage were monitored. Females of *A. franklinii* and *P.t. tasmanicus* were held in environmental

chambers where photoperiod, air and water temperatures were controlled. Incubation and development of eggs were studied at seasonal temperatures, 10°C and 15°C. *A. gouldi* females were held in an artificial pond at ambient temperature. Development of eggs/young was checked every day, and a small number of eggs or young were removed periodically for detailed observation of developmental stages. As *Astacopsis* females appeared susceptible to stress, handling was reduced to minimize brood loss.

Sexual maturity in females was determined by the presence of abdominal eggs or young, ovarian condition prior to and during mating season as well as the presence and degree of development of secondary sexual characteristics (ie: sexually mature female exhibited fully developed secondary sexual characters). Mature males were those which had spermatophores containing sperm tubes within their vasa deferentia prior to and during mating season.

Due to the biennial reproductive cycle which became apparent when the two genera were examined, specific nomenclature had to be used when referring to sexually mature females: females breeding in a given season are referred to as "reproductive" while those not breeding that same season are termed "nonreproductive". Ovigerous females (carrying abdominal eggs) are also referred to as "berried" or "in berry".

6.3 RESULTS

6.3.1 Maturity size

A. Astacopsis gouldi

In the Inglis River population 10 males (CPL 63 to 110.5 mm) were examined during the mating season. The smallest individual with spermatophores in the vasa deferentia measured 76.0 mm CPL while the largest without spermatophores measured 77.0 mm CPL. Of the 247 females captured during this study 13 were mature and of these only 6 were in berry. The smallest of the berried females measured 119.0 mm CPL while the largest was 163.0 mm (mean =135.9, s.d. = 19.4). The smallest nonberried mature female measured 118.6 mm CPL. Females showing partial development of secondary sexual characters (ie: lightly setose

gonopore and partially decalcified tail fan and gonopore cover), ranged from 107.0 to 119.5 mm CPL. The largest immature female caught (ie: small ovary, closed nonsetose gonopore and calcified tail fan) measured 118.5 mm CPL.

Mature females collected from other sites fell well within the size range observed in the Inglis River (ie: CPL \geq 120 mm were mature).

Females therefore begin to acquire sexual characters around 107 mm CPL but do not mature fully until 119 mm CPL. All females CPL \geq 120 mm were sexually mature. The number of males examined was small but it appears that spermatophore production occurs in individuals of CPL \geq 76 mm.

B. *Astacopsis franklinii* Eastern form

Figure 6.1 shows the size range of mature males captured in the Mt. Wellington populations as determined by the presence of sperm in their gonoducts. The smallest male with sperm in the vasa deferentia measured 29.0 mm CPL while the largest male without sperm measured 37.7 mm CPL.

Of the 436 females captured from the two main Mt. Wellington populations, 118 were mature and of these 45 were carrying eggs or young (Figure 6.2). In Hobart Rivulet the smallest ovigerous female measured 42.5 mm CPL and the largest 56.0 mm CPL (mean = 47.5, s.d. = 2.8, n = 29) while in Guy Fawkes Rivulet the smallest measured 39.2 mm CPL and the largest 53.0 mm CPL (mean = 44.3, s.d. = 4.1, n = 16). Females showing partial development of secondary sexual characters ranged from 36.0 to 46.0 mm CPL. The largest female without any sexual characters (ie: no oosetae, closed nonsetose gonopore and calcified tail fan) caught measured 40 mm CPL. Only 31.8 % of females were mature at CPL 39-40 mm but by CPL 45-46 mm, 67.9 % were mature and at 47 mm CPL 100% were mature.

Females collected in New Town Rivulet (Mt. Wellington) displayed a similar range in maturity size with mature females' CPLs ranging from 43.5 to 52.6 mm. The largest immature female captured at this site measured 40.0 mm CPL and females showing partial development of secondary sexual characters ranged from 38.5 to 44.0 mm CPL.

In the streams of Mt. Wellington, females therefore begin to acquire secondary sexual characters between 36 and 46 mm CPL but most do not mature until 46 mm CPL. Males apparently begin to produce sperm at approximately 30 mm CPL but 100% maturity is not reached until size classes of CPL \geq 38 mm.

Figure 6.1 Number of males with and without spermatophores in preserved samples from the Mt. Wellington populations of *A. franklinii* prior to and during the mating season.

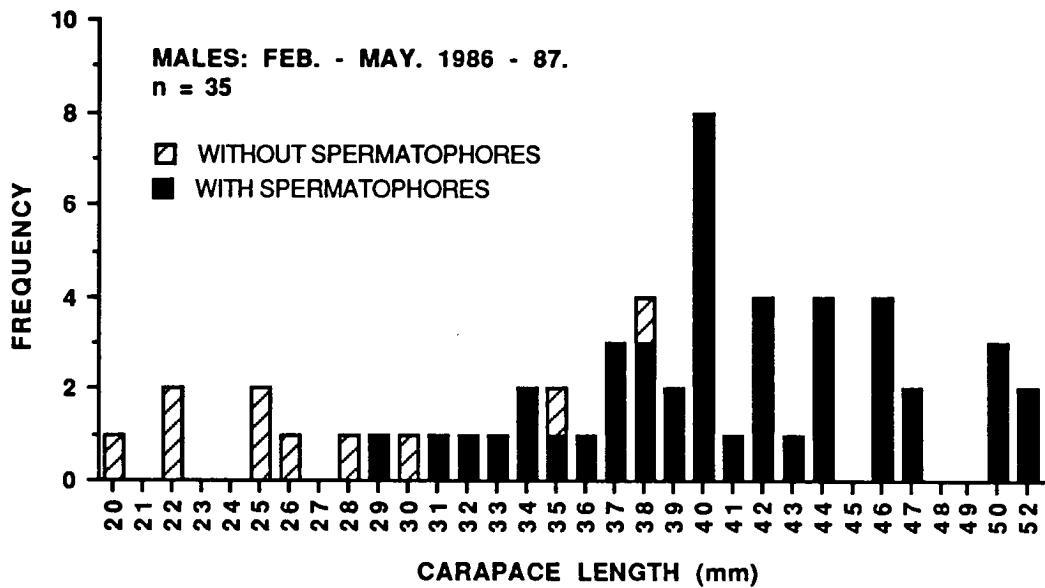
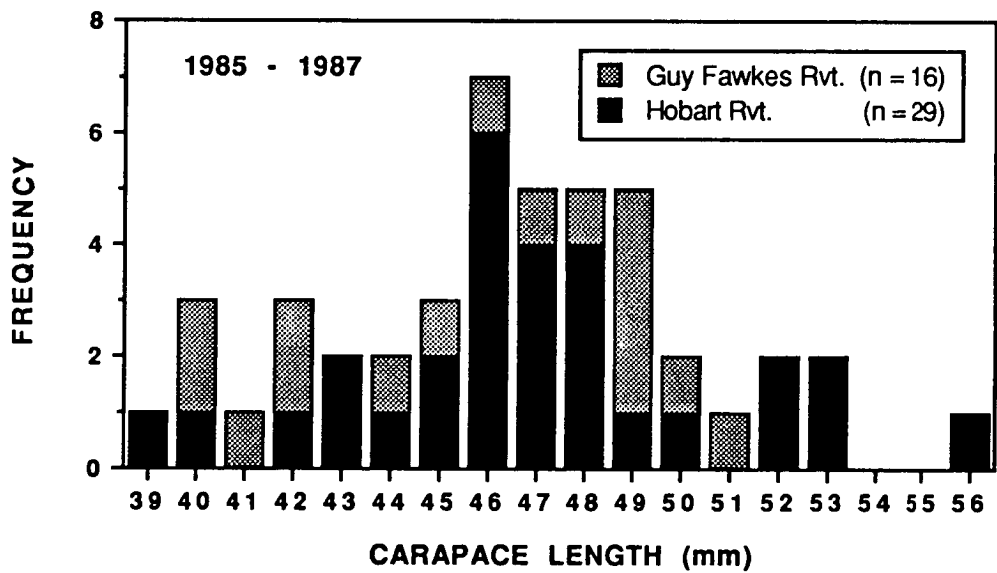


Figure 6.2 Number of *A. franklinii* females in berry from the two Mt. Wellington populations captured from September 1985 to May 1987.



***C. Astacopsis franklinii* Western form**

Samples of the Clarence Lagoon population were taken in January 1986 and February 1987 (n total = 111). Of the 67 females collected 28 were sexually mature (CPL range 62.0 - 75.6 mm). Only one of these was berried (CPL 75.6 mm). Females showing partial development of secondary sexual characters ranged from 54.0 to 67.0 mm CPL. The largest immature female caught measured 58.0 mm CPL. Males ranged in CPL from 30.0 mm to 90.5 mm but the size of sexual maturity could not be established as samples were not taken during the breeding season.

In the Lake Meston sample (Feb. 27, 1986; n = 15) the four mature females ranged from 80.0 to 91.0 mm CPL. The largest immature female measured 64.5 mm CPL. Males (n = 11) ranged in CPL from 54.5 to 98.0 mm. Spermatophore formation was in the early stages in all mature specimens but the smallest male with sperm within the vasa deferentia measured 79.0 mm CPL.

Pelverata Falls was sampled in January and April 1987 (n total = 33). None of the females (n = 16) captured were mature. Two females (CPL 52.0 and 51.5 mm) showed partial development of secondary sexual characters. Immature females ranged from 26.0 to 41.2 mm CPL. Males (n = 17) ranged in CPL from 22.0 to 57.2 mm. The smallest individual with sperm within the vasa deferentia measured 35 mm CPL while the largest without measured 36.5 mm CPL.

A small sample taken from the Lower Gordon River (Apr. 1988; n = 6) contained two mature females CPL 101.0 mm and 112.0 mm. The one immature female measured 106.8 mm CPL. The size of sexual maturity in males (CPL 99, 125.5 and 148.4 mm) was not established.

Overall, the size of sexual maturity appears variable in populations of the Western form. Females begin to acquire secondary sexual characters between 52 and 67 mm CPL. Sexually mature females range in size from 62 to 112 mm CPL. The number of males examined was small but it appears that, at least in some populations, spermatophore production occurs in individuals of CPL \geq 37 mm.

***D. Parastacoides t. tasmanicus* (SP)**

Figure 6.3 shows the size range of mature males in the Harlequin Hill population as determined by the presence of sperm in their gonoducts. The smallest male with sperm in the vasa deferentia measured 16 mm CPL while the largest male

Figure 6.3 Number of males with and without spermatophores in preserved samples from the Harlequin Hill population of *P. t. tasmanicus* (SP) prior to and during the mating season.

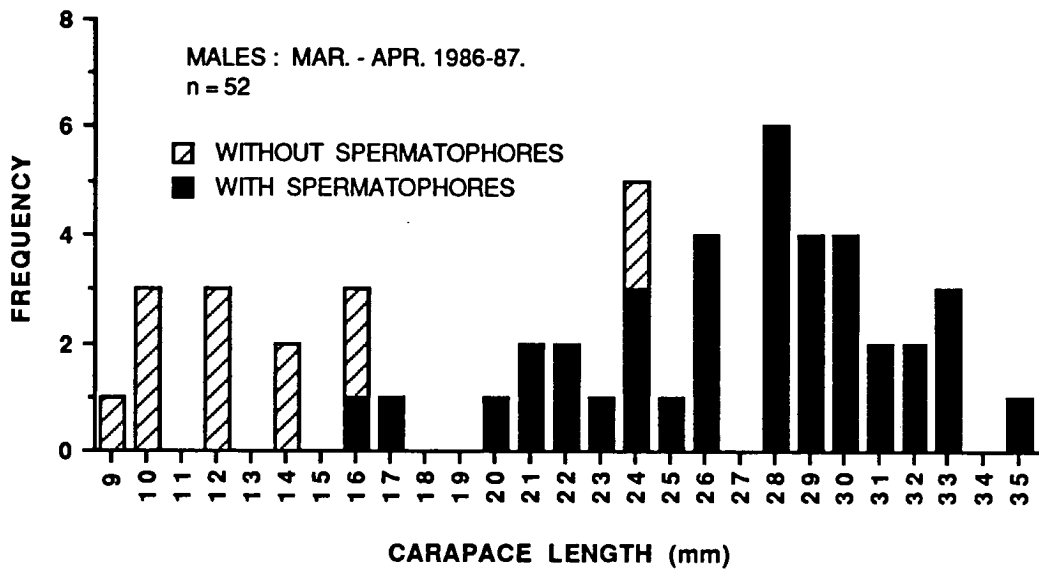
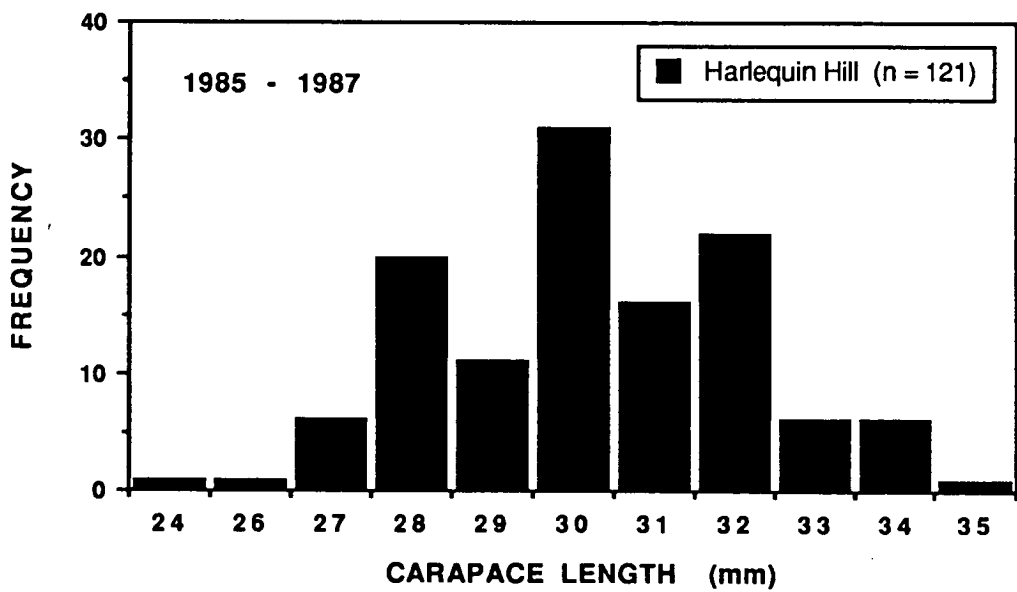


Figure 6.4 Number of *P. t. tasmanicus* (SP) females in berry from the Harlequin Hill population captured from April 1985 to April 1987.



without sperm measured 24.0 mm CPL.

Of the 754 females captured at Harlequin Hill, 520 were mature and of these 121 had abdominal eggs or young (Figure 6.4). The smallest measured 23.6 mm CPL while the largest was 35.0 mm CPL (mean = 30.2, s.d. = 2.0). The smallest nonovigerous reproductive female measured 23.0 mm CPL. Only 14.3 % of females were mature at CPL 23-24 mm but by CPL 27-28 mm, 72.7 % were mature and at CPL 30 mm 100% were mature. Females showing partial development of secondary sexual characters ranged from 26.3 to 30.5 mm CPL. The largest female caught without any sexual characters (ie: no oosetae, closed nonsetose gonopore) measured 29.8 mm CPL.

Females therefore first begin to mature between 23 and 29 mm CPL but the majority do not breed until 30 mm CPL. Males apparently begin to produce sperm at approximately 16 mm CPL but 100% maturity is not reached until size classes of CPL ≥ 25 mm.

E. *Parastacoides t. tasmanicus* (N)

Samples from the Needles population were taken in October 1985, October 1987 and March 1988 (n total = 76). Of the 21 females collected, 18 were mature and of these 9 were carrying broods. The smallest of the brooding females measured 27.5 mm CPL while the largest was 32.0 mm CPL (mean = 29.9, s.d. = 1.76). The smallest nonovigerous mature female measured 26.2 mm CPL while the largest immature female measured 26 mm CPL.

Males ranged from CPL 17.1 to 32.5 mm and only a small number of larger males was checked for sperm development. Of these all individuals of CPL ≥ 26 mm had sperm in their vasa deferentia during the mating season.

F. *Parastacoides t. insignis*:

Samples from the Scotts Peak Dam population were taken in October 1985, January 1986 and October 1986 (n total = 32). Of the 20 females collected, 11 were mature and of these 4 were carrying broods. The smallest of the brooding females measured 23.0 mm CPL while the largest was 27.2 mm CPL (mean = 25.4, s.d. = 1.77). The smallest immature female showing partial development of secondary sexual characters (ovisetae, decalcified and setose gonopore) measured 22.0 mm CPL while the largest female without any development of these characters measured 23.5

mm CPL.

The size of sexual maturity in males (CPL 19.5 to 27 mm) was not established.

G. Parastacoides t. inermis

Overall, seven samples were taken from the Harlequin Hill area between July 1985 and January 1987 (n total = 81). Of the 42 females collected 22 were mature and of these 13 were carrying broods. The smallest of the brooding females measured 17.0 mm CPL while the largest was 26.0 mm CPL (mean = 23.1, s.d. = 2.49). The smallest immature female showing partial development of secondary sexual characters (ovisetae, decalcified and setose gonopore) measured 16.4 mm CPL while the largest female without any development of these characters measured 17 mm CPL.

Males ranged from 9 to 26 mm CPL and all those of $\text{CPL} \geq 18$ mm had sperm in their vasa deferentia during the mating season.

6.3.2 Seasonal breeding cycle of mature animals

A. Astacopsis gouldi

In the samples taken from various sites between October 1985 and March 1988, berried females occurred from October to January while females carrying young were caught from December to April.

In the Inglis River, none of the 6 mature females captured carried broods during the spring/summer of 1985-86. The following season (1986-87), 6 females with broods and 3 without broods were caught. Two of the ovigerous females were recaptured from the previous year and had come into berry sometime between autumn and spring 1986. Berried females were captured in early December when eggs contained embryonized protozoas (see Chapter 7) and in mid-January when fully formed embryos with pigmented eyes were about to hatch. Young hatched from mid-January to early February when females (including one recapture from December) carried very early stage 1 young. One female with early stage 2 young was captured on March 5 and then again on April 19 by which time her young had moulted to stage 3. From this it can be concluded that the duration of stages 2 and 3 was at least 45 to 50 days at temperatures ranging from 7 to 18 °C. Free living stage 3 young were not

captured but were probably released in late April.

Incubation of eggs and young by three berried females captured at Wilson's Creek (October 1985), W. Gawler River (November 1985) and Detention River (November 1986) was monitored in the laboratory. The eggs of these females ranged from 4.7 to 5.7 mm in length and 3.5 to 4.2 mm in width and hatched between December 9 to 12 in all three females. At temperatures ranging from 12 to 19 °C the young spent 9 to 13 days in (early and late) stage 1 and then moulted to stage 2. Following a further 7 to 10 days they moulted to stage 3 in which they remained for 35 days before moulting to stage 4. Stage 3 young began venturing away from the mother after 28 days but most returned to reattach to her abdomen. They became truly independent only after the moult to stage 4, although some young of the later stage were observed returning to the female for a further 12 days.

The two berried females captured in October-November 1985 were kept in the artificial pond at the University laboratory. Both of these females moulted the following summer, approximately one year after releasing their broods, and then mated again in autumn. One female moulted on December 31, 1986 and mated and spawned on April 1, 1987 while the other moulted on February 15, 1987 and mated and spawned on May 1, 1987. One brood was lost but in the other, eggs were carried over winter and hatched in early December 1987.

During the mating season, nonreproductive females were characterized by the loss of setae around the gonopore (see Fig. 5.6H), lack of glair glands, general wear of abdominal setae, dirty exoskeletons (ie: not recently moulted), small ovaries and the presence of eggs stalks on pleopods. Reproductive females on the other hand had well developed glair glands, heavy setation around the gonopore (see Fig. 5.6G), clean dense abdominal setation, large brown ovaries, clean exoskeletons (ie: recently moulted) as well as long clean oosetae on the pleopods. Reproductive setation of the abdomen, gonopores and pleopods was therefore fully or partially lost during the long female cycle but was reacquired in the pre-reproductive moult.

Glair gland development was noted in laboratory females approximately one month before extrusion. Glair gland development could not be followed in the field because of the infrequent capture of mature females especially prior to spawning.

It appears therefore that mature females of this species mate and spawn in autumn, carry their eggs and young until well into the following summer, release their broods and overwinter, then moult in mid summer and mate and spawn again in

autumn, two years after their previous mating.

A small number of sexually mature males was sacrificed throughout the year at various sites to check for spermatophore formation. Sperm was found in the vasa deferentia of six males sacrificed from February to May while three mature males sacrificed in November had no sperm in their gonoducts. During and prior to the mating season spermatophores, consisting of coiled sperm tubes embedded in a clear granular matrix, can be seen in the round and swollen vasa deferentia of mature males (Fig. 6.5B&C). The numerous spermatozoa seen within the sperm tubes are round, conspicuously nucleated and lacking the rays characteristic of the sperm of other Astacidea. In contrast, the vasa deferentia of mature males collected in the spring were flattened, deflated and contained only a small amount of the granular matrix (Fig. 6.5A).

The ovarian and testicular cycles were not documented in detail because of the small number of mature individuals in the Inglis River population. As this site was subject to heavy recreational fishing in the past the number of adults was low and regular sacrifice of the few remaining adults would severely damage the population.

B. *Astacopsis franklinii* (Eastern form)

In the samples taken from Hobart and Guy Fawkes rivulets between September 1985 and May 1987, berried females occurred from April to February while females carrying young were caught from February to May (Fig. 6.6).

Glair gland development (in reproducing females) was first detected in preserved samples from February. The glands were only weakly developed and could be observed clearly only under a dissecting microscope. In field collections, glair gland development was first noted in March and reached a peak in late April - early May when the conspicuous glands were easily detected by casual inspection of the abdomen. Glair glands were still noted in several females just after egg extrusion but disappeared within a month of spawning.

Mating and spawning occurred from late April to early May when courting and copulating pairs as well as females with attached spermatophores (see Chapter 7) and freshly extruded eggs were found. Eggs were carried through the winter and until the early spring (Sept. to Oct.) little or no embryonic development was observed. In November eggs with embryonized nauplii were seen on berried females and by December the eggs contained embryos in the protozoal development stage (See

Figure 6.5 Cycling of male gonad anatomy in *A. gouldi*:

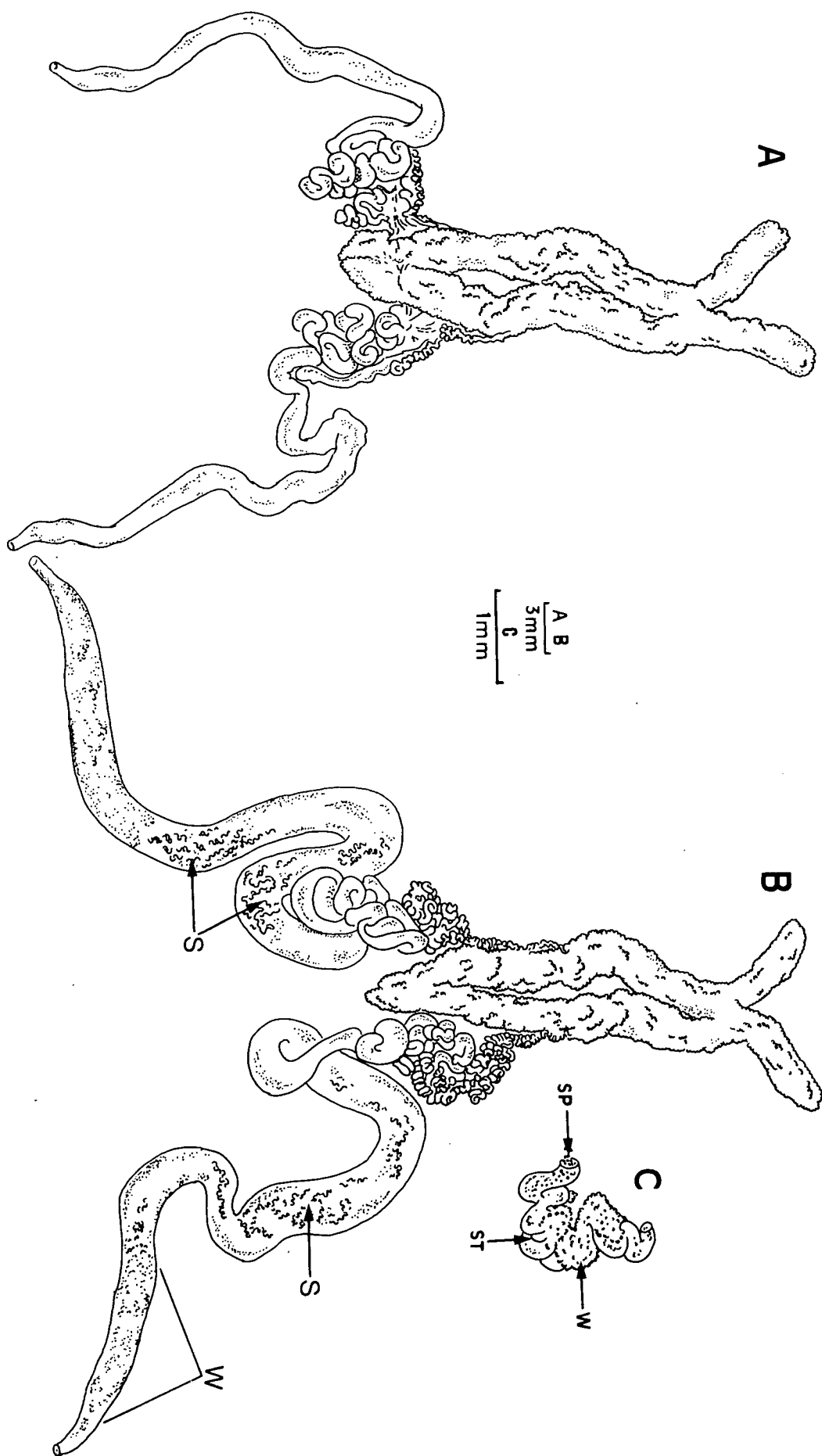
A. Testes and vasa deferentia of male CPL 114.5 mm. Captured 20.11.1987. Note absence of sperm tubes.

B. Testes and vasa deferentia of male CPL 111.0 mm. Captured 15.5.1987.

S = region containing sperm tubes within matrix

W = region containing matrix only.

C. Detail of sperm tube (st) showing sperm (sp) and surrounding matrix (w).



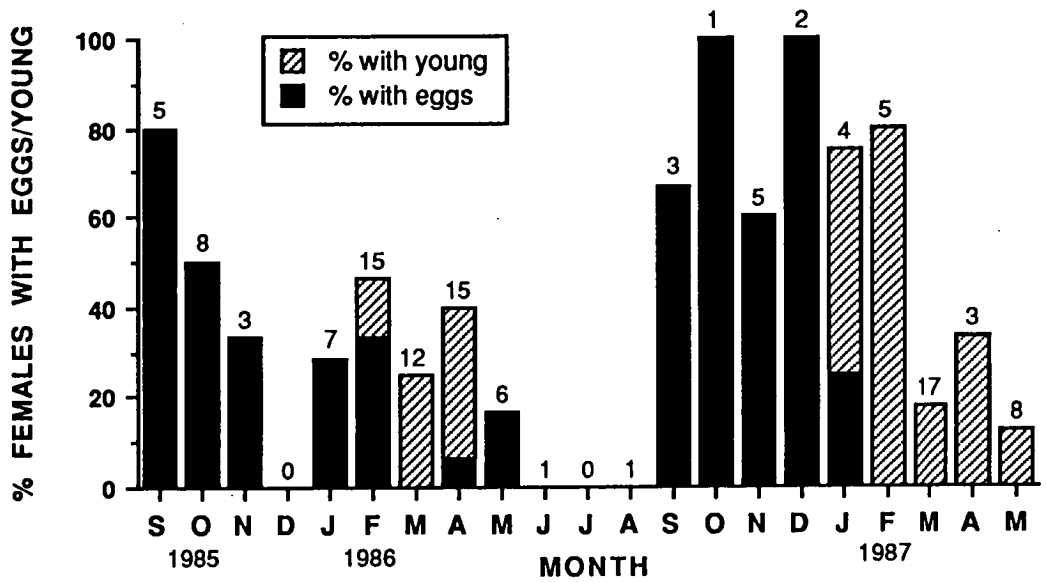


Figure 6.6 The percentage of mature *A. franklinii* females with eggs and with young (stages 1-3) captured in Mt. Wellington streams from September 1985 to May 1987. (Numeral on top of columns indicates the number of mature females in monthly samples.)

Chapter 7). Hatching occurred between mid January and mid February when females carrying eggs with fully developed embryos and/or early stage 1 young were found (Fig 6.6). Females carrying stage two young were collected in mid February from Guy Fawkes Rivulet and in mid March from Hobart Rivulet while attached stage three young were found from late February to mid March in Guy Fawkes and mid April to early May in Hobart Rivulet. The young crayfishes appeared to leave their mothers from mid to late March in Guy Fawkes Rivulet and late April to early May in Hobart Rivulet when (nonreproductive) females without broods and females with small broods of late stage three young were captured.

In the laboratory mating pairs, copulation and spawning occurred from early May to mid June. The development of eggs and young of the broods of 15 females collected at various times of the year (Sept.-Jan.) were monitored in the laboratory at seasonal air temperatures. Eggs hatched from November to February. Eggs of females captured in September took 60 to 65 days (at 12-17°C) to hatch while those of females captured in early January only took 10 to 17 days (at 15-19°C). At temperature ranging from 15 to 19°C stage 1 lasted 10.5 days (s.d. = 1.9, range = 8 - 13), stage 2 required 8.4 days (s.d. = 1.7, range = 6 - 10) and stage 3 took 25.6 days (s.d. = 4.3, range = 18 - 34). Six ovigerous females were also kept in a 10°C constant temperature room. The eggs of these females took much longer to hatch (eggs from females captured in September took 111 days, while those captured in December took 97 days) and the survival rate of young was poor with no broods surviving past stage 2. Stage 1 lasted 25 to 35 days while stage 2 lasted approximately 20 days.

As in *A. gouldi*, mature females of *A. franklinii* bred biennially. The representative female reproductive cycle is shown in Figure 6.7. Females which carry a brood in a given summer are therefore termed nonreproductive as they will not be mating and spawning at the end of that summer. During each breeding season only approximately 50 % of mature females spawn in a given population. In the 1985 - 86 season, 65.5 % of mature females spawned in Hobart Rivulet and 56.6 % in Guy Fawkes Rivulet while in 1986 - 87, 45.5 % spawned in Hobart Rivulet and 46.4 % in Guy Fawkes Rivulet. Overall (both streams: 1985-87) 54.1% were noted as reproductive and 45.9 % as nonreproductive (n total = 109). The fluctuations in the breeding component of the population are influenced by the number of females attaining maturity in a particular summer, eg: in 1985-86 a large number of females

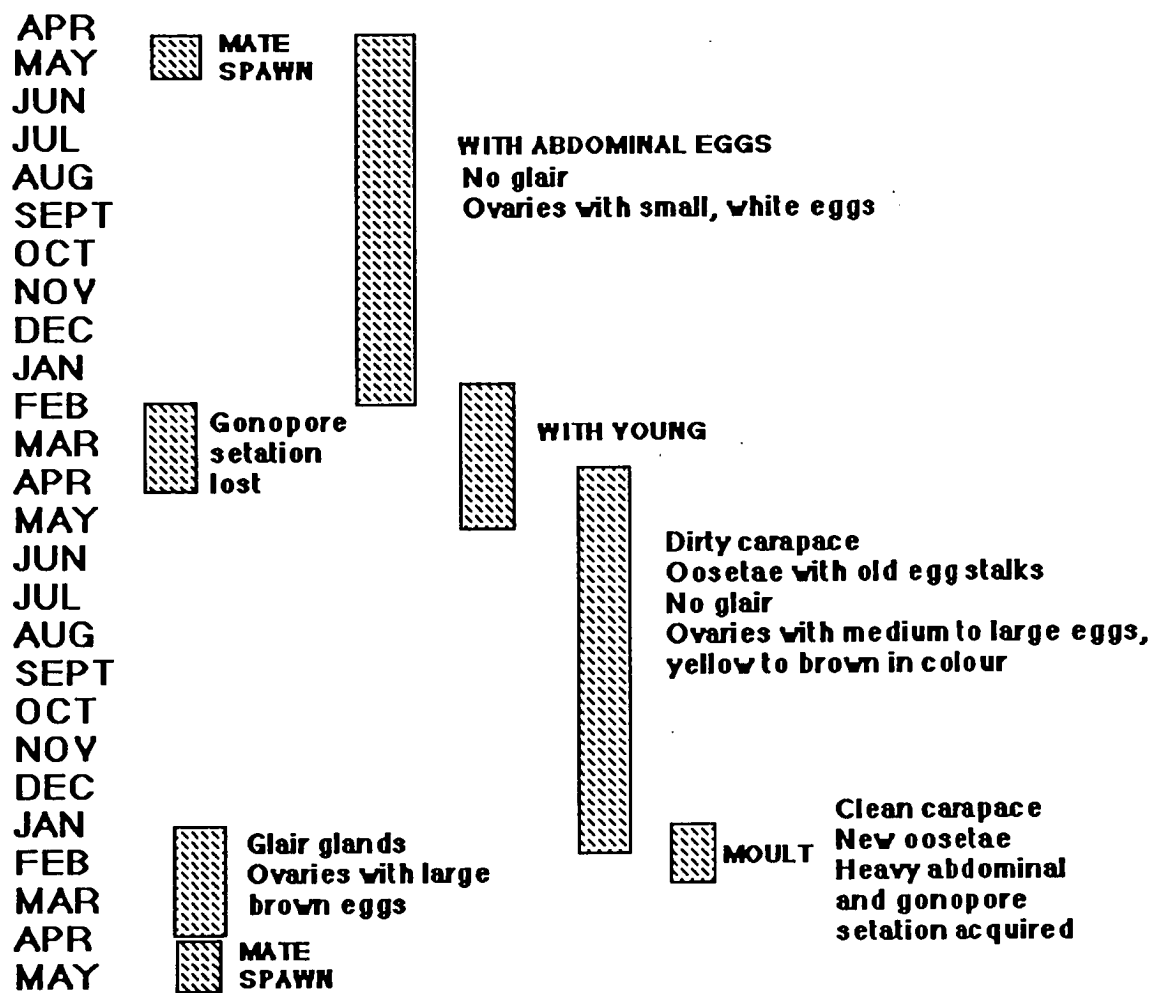


Figure 6.7 The typical biennial reproductive cycle of mature *A. franklinii* females in Mt. Wellington streams.

matured, thus bolstering the reproductive portion. Reproductive and nonreproductive females were present in both populations at all times of the year. There was no difference in size between the breeding and nonbreeding groups ($t = 0.52$, $df = 100$, $p < 0.60$). The mean CPL of females which bred in 1985-86 was 45.7 mm (s.d. = 3.9, range = 39.7 - 51.6, $n = 56$) while that of females which bred in 1986-87 was 46.1 mm (s.d. = 3.2, range = 38.5 - 56.0, $n = 46$).

During and prior to the mating season, nonreproductive females were characterized by the loss of setae around the gonopore (see Fig. 5.7E), lack of glair glands, general wear of abdominal setae, dirty exoskeletons (ie: not recently moulted), small to medium yellow ovaries and the presence of eggs stalks on pleopods (Fig. 5.19B). In contrast, reproductive females had well developed glair glands, heavy setation around the gonopore (see Fig. 5.7D), clean dense abdominal setation, large brown ovaries, clean exoskeletons (ie: recently moulted) as well as long clean oosetae on pleopods (Fig. 5.19A).

The growth of ova through the ovarian cycle could not be documented monthly because of the small number of mature individuals preserved outside the mating season. Ovarian eggs at the beginning of their cycle (ie: those of females less than a month after spawning) had mean length of 0.69 mm (s.d. = 0.23) and a mean width of 0.52 mm (s.d. = 0.17). Approximately two years later just prior to being extruded, the eggs measured 3.55 mm (s.d. = 0.38) in length and 2.32 mm (s.d. = 0.21) in width. The ovarian cycle of mature females is summarized in Figure 6.8A. The average lengths and widths of ovarian eggs from crayfishes collected between February and May differed significantly between reproductive and nonreproductive females (length: $t = 6.8$, d.f. = 19, $p < 0.0001$, width: $t = 3.5$, d.f. = 19, $p < 0.003$). The mean egg length of reproductive females at this time was 3.44 mm (s.d. = 0.31, $n = 120$) while the egg width was 2.22 mm (s.d. = 0.51, $n = 120$). In nonreproductive females captured during this time, the mean egg length was 2.01 mm (s.d. = 0.58, $n = 90$) and the mean egg width was 1.45 mm (s.d. = 0.40, $n = 90$). Similarly the ovary weights of reproductive females were significantly heavier at this time (mean ovary weight: rep. fem. = 0.96 g, s.d. = 0.4; nonrep. fem. = 0.51 g, s.d. = 0.25; $t = 3.23$, d. f. = 19, $p < 0.004$). The biennial breeding cycle was confirmed in the laboratory by long term observation of five females used initially for brood incubation experiments. The ovary development and moulting pattern of these females mirrored the cycle outlined in Figure 6.7. Multiple field recaptures of two of

Figure 6.8 Ovarian cycle of *A. franklinii* and *P. t. tasmanicus*.

A. *A. franklinii* (Guy Fawkes Rivulet).

1. Ovary of reproductive female, CPL 45.5 mm, just prior to spawning (4.4.1986). Ovary weight: 1.1 grams; mean egg length: 3.9 mm (s.d. = 0.2); mean egg width: 2.6 mm (s.d. = 0.2).
2. Ovary of berried female, CPL 47.5 mm, just after spawning (30.4.1986). Ovary weight: 0.14 grams; mean egg length: 0.69 mm (s.d. = 0.2); mean egg width: 0.52 mm (s.d. = 0.2).
3. Ovary of nonreproductive female, CPL 46.6 mm, just after the release of young (27.2.1987). Ovary weight: 0.30 grams; mean egg length: 1.9 mm (s.d. = 0.4); mean egg width: 1.3 mm (s.d. = 0.3).

B. *P. t. tasmanicus* (Harlequin Hill).

1. Ovary of reproductive female, CPL 30.0 mm, just prior to spawning (27.2.1986). Ovary weight: 0.37 grams; mean egg length: 2.77 mm (s.d. = 0.33); mean egg width: 2.07 mm (s.d. = 0.3).
2. Ovary of berried female, CPL 31.0 mm, just after spawning (9.4.1986). Ovary weight: 0.03 grams; mean egg length: 0.50 mm (s.d. = 0.10); mean egg width: 0.29 mm (s.d. = 0.05).
3. Ovary of nonreproductive female, CPL 31.0 mm, just after the release of young (13.3.1987). Ovary weight: 0.04 grams; mean egg length: 0.85 mm (s.d. = 0.17); mean egg width: 0.64 mm (s.d. = 0.09).

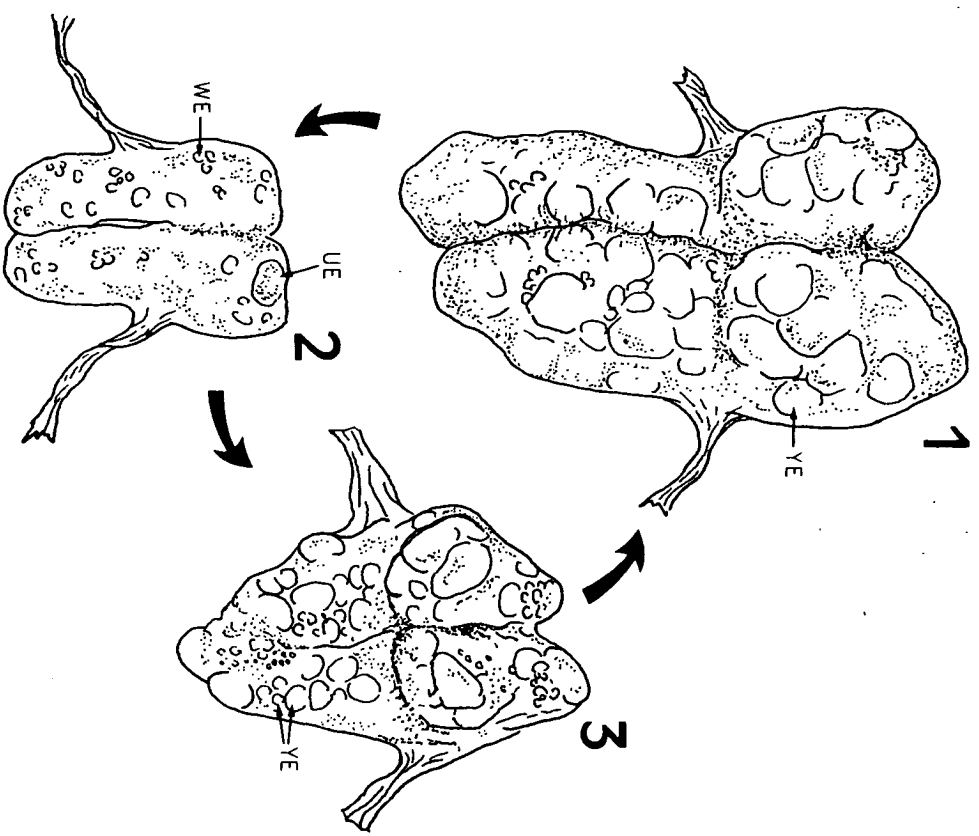
Abbreviations:

YE = yolky eggs

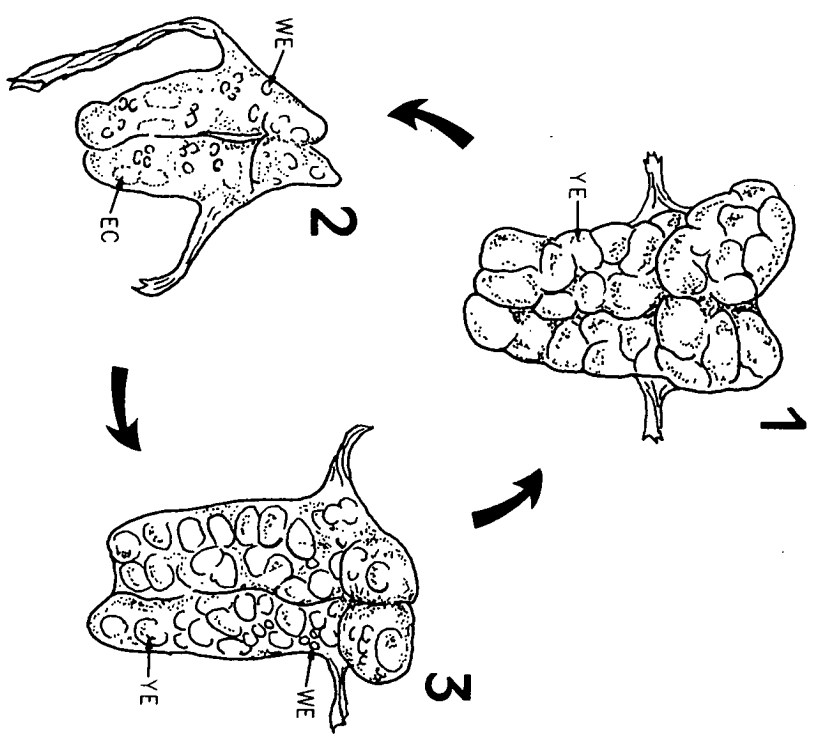
WE = white eggs without yolk

UE = unextruded eggs

EC = ovarian egg capsules of extruded eggs



5 mm



A: Astacopsis

B: Parastacoides

the marked mature females also showed this cycle.

Abdominal eggs ranged from 3.19 to 3.90 mm in length and 2.59 to 3.2 mm in width (Fig. 6.9). Larger females carried overall larger abdominal eggs: when the average egg diameters of females $CPL \geq 46$ mm were compared to those of females $CPL \leq 45$ mm there was significant difference in size between the two groups ($t = 3.14$, d.f. = 19, $p < 0.005$). Abdominal eggs increased in both length and width during incubation. The eggs of berried females collected in September - October had a mean length of 3.55 mm (s.d. = 0.17) and a mean width of 2.78 mm (s.d. = 0.14) while those collected in January - February had a mean length of 3.76 mm (s.d. = 0.13) and a mean width of 3.07 mm (s.d. = 0.11). These seasonal differences in the eggs' dimensions, although small, were statistically significant (length: $t = 2.3$, $df = 13$, $p < 0.038$; width: $t = 3.99$, $df = 13$, $p < 0.002$).

The mean ovary weight of immature females was smaller than that of mature females throughout the year ($t = 12.1$, $df = 62$, $p < 0.0001$). In very small females ($CPL \leq 30$ mm) the ovaries were very small with small, yolkless ova and mean weight of 0.006 g (s.d. = 0.005). In some of the larger immature females ($CPL > 30$ mm), ovaries began to develop and ova were larger, with various concentrations of yolk and a mean ovary weight of 0.159 g (s.d. = 0.19) (Fig. 6.10). Some of these females were approaching the maturity moult and thus their ovaries were at a similar developmental stage as were the ovaries of reproducing females.

Sperm was found in the vasa deferentia of males from February to May. Sperm tubes began forming in February, their number peaked in early May and decreased through the winter (Table 6.1). As in *A. gouldi*, spermatophores consisted of sperm tubes embedded in a clear matrix. The anatomy of the gonads of reproductively active and inactive males was identical to that described for *A. gouldi* (Fig. 6.5). The diameters of the vasa deferentia (the distal portions in particular) were small and the overall weights of the gonads were low in mature males in the spring but increased with the approach of the mating season (Fig. 6.11). Gonad weight was greatest in May (mean = 0.50 % body wt., s.d. = 0.21) and lowest in November (mean = 0.09 % body wt. s.d. = 0.004) while the diameter of the vasa deferentia was largest in May (mean = 1.84 mm, s.d. = 0.67) and smallest in January (mean = 0.86 mm, s.d. = .089). The gonad weights and vasa deferentia diameters of males with spermatophores (February to May) were significantly larger than those without spermatophores (October to January), (Vas deferens diameters: $t = 3.78$, d.f. = 77, p

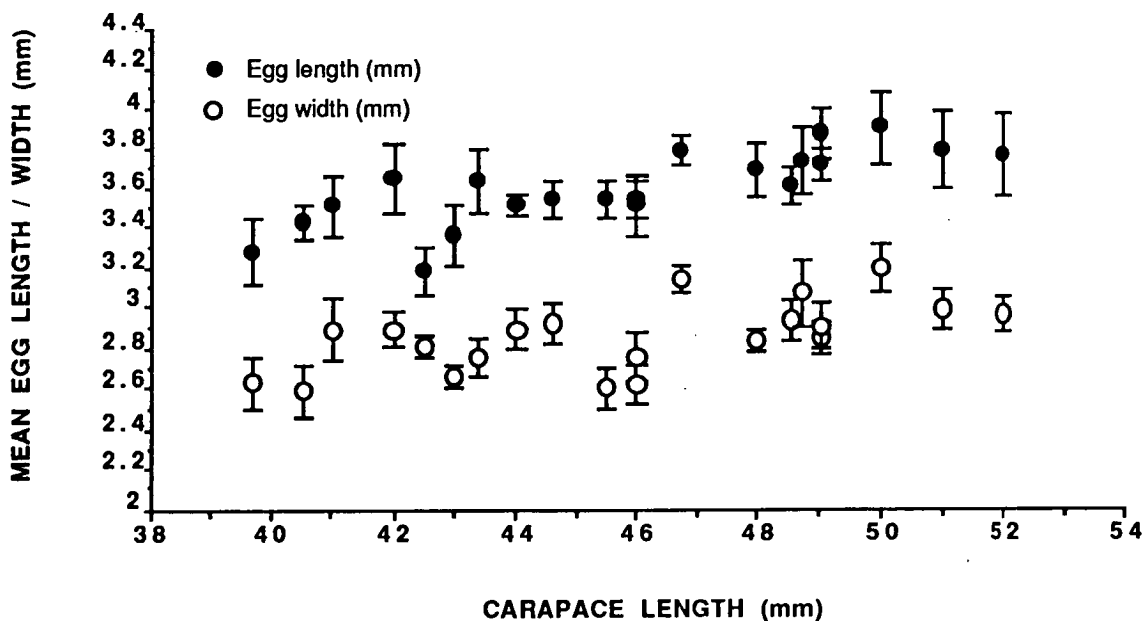


Figure 6.9 Mean abdominal egg length and width in berried females collected from Hobart and Guy Fawkes Rivulets from September 1985 to May 1987 (n = 21 broods, 167 eggs).

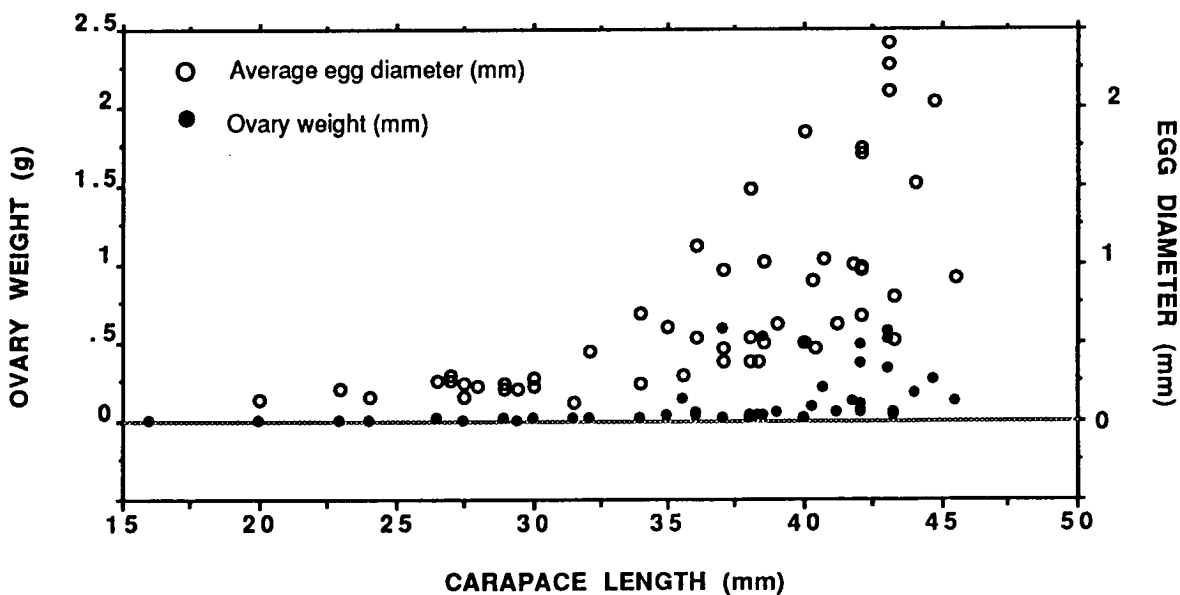


Figure 6.10 Average egg diameter and ovary weight of immature females collected from Hobart and Guy Fawkes Rivulets (n = 54).

Table 6.1. Spermatophore development in the yearly reproductive cycle of male *Astacopsis franklinii* from Mt. Wellington streams.

OCTOBER	Vas deferens flat and empty.
NOVEMBER	little or no matrix.
DECEMBER	No sperm tubes
JANUARY	
FEBRUARY	Vas deferens rounder, fuller,
MARCH	with matrix and sperm tubes moderate to abundant.
APRIL	Vas deferens round, very full.
MAY	Matrix abundant. Sperm tubes numerous with sperm within.
JUNE	Condition unknown.
JULY	Spermatophores
AUGUST	degenerating?
SEPTEMBER	Vas deferens still round but mostly empty. Sperm tubes empty, very low in number.

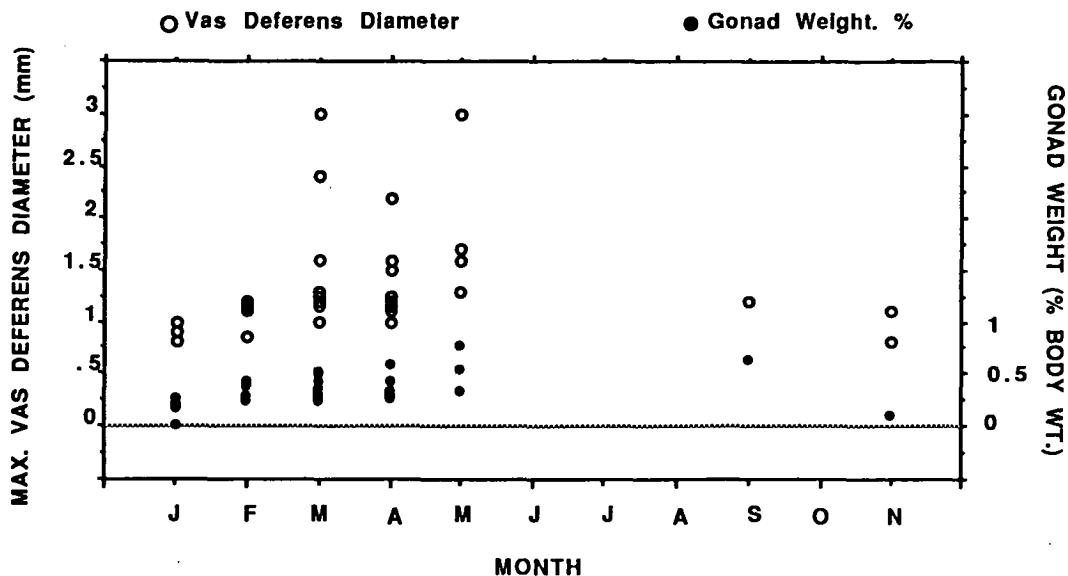


Figure 6.11 Monthly variation in the maximum diameter of the vasa deferentia and gonad weight (expressed as the percentage of total body weight) in mature *A. franklinii* males (CPL ≥ 39 mm) from Mt. Wellington streams (n = 40).

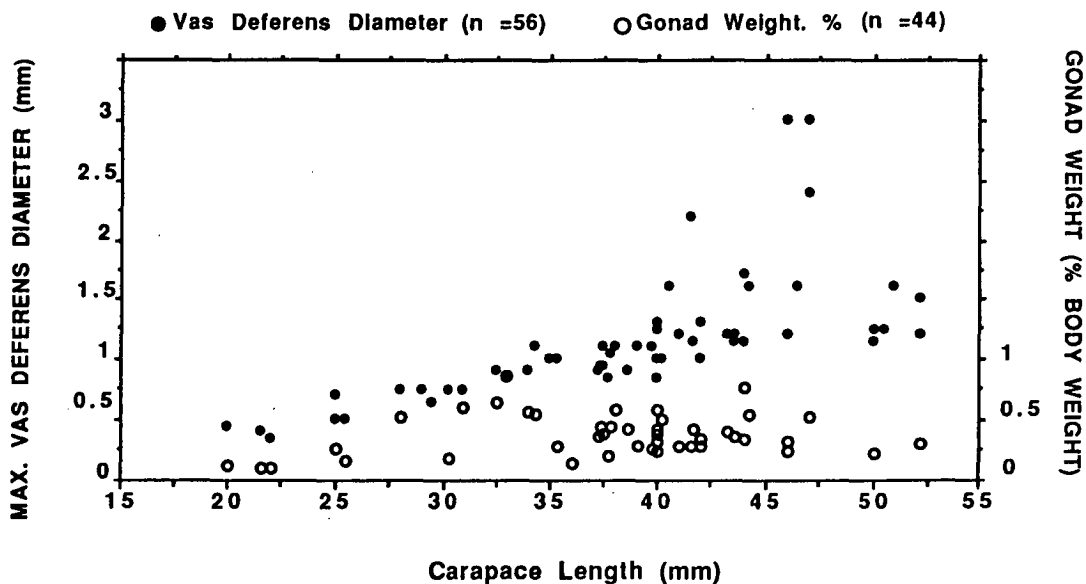


Figure 6.12 The relationship between carapace length, maximum diameter of the vasa deferentia and gonad weight (expressed as the percentage of total body weight) in mature and immature *A. franklinii* males (collected February to May) from Mt. Wellington streams.

< 0.0003 ; Gonad weight: $t = 4.78$, d.f. = 78, $p < 0.0001$).

Gonad weights and vasa deferentia diameters increase with size but a considerable variability occurs in reproductive males. The largest vas deferens diameters were recorded in reproductive mature males of CPL 40 to 47 mm (Fig 6.12). The gonad weights and vasa deferentia diameters of mature males were significantly larger than those of immature males. In males preserved during and prior to the mating season, the mean diameter of the vasa deferentia of mature individuals was 1.29 mm (s.d. = 0.28) while that of immature individuals was 0.71 mm (s.d. = 0.53) : $t = 3.73$, d.f. = 53, $p < 0.0005$. The mean gonad weight (expressed as percent of body weight) of mature males at this time was 0.41 (s.d. = 0.16) while that of immature males was 0.21 (s.d. = 0.14): $t = 3.15$, d.f. = 41, $p < 0.003$.

In summary, mature females of *A. franklinii* (Eastern form) mate and spawn in autumn (May), carry their eggs and young until well into the following autumn (April - May), release their broods and overwinter, then moult in mid summer and mate and spawn again in autumn, two years after their previous mating. This biennial breeding pattern results in two distinct female reproductive groups: 1. reproductive = those moulting, mating and spawning in a given summer and 2. nonreproductive = those incubating young and larvae. The two groups can be easily separated on the basis of ovary development, presence of eggs or young and condition of secondary sexual characters. The gonads of reproducing females and males show synchronous cyclic development with peak development occurring just prior to the mating season. Larger females carry larger abdominal eggs which increase in size during the period of incubation. The rate of development of eggs and young is directly influenced by water temperature with higher temperatures causing accelerated development.

C. Astacopsis franklinii (Western form)

Since none of the populations were sampled on a regular basis, little can be said about the seasonality of breeding of this form. Females however also appear to breed biennially as both reproductive and nonreproductive mature females were present in the samples taken at both Clarence Lagoon and Lake Meston. Females carrying stage 2 and 3 young were collected in February in Lake St Clair and Lake Meston respectively. None of the mature sized males collected in January from Clarence Lagoon had spermatophores in their vasa deferentia but some of the large males from

Lake Meston (February) showed early spermatophore formation.

D. *Parastacoides t. tasmanicus* (SP)

In samples taken from the Harlequin Hill site between April 1985 and April 1987, berried females occurred from April to November while females carrying young were caught from November to January (Fig. 6.13).

Glair gland development (in reproducing females) was first detected in preserved samples from February when 25% of reproducing females examined showed some gland development. In the field, glair gland development was first noted in March just prior to the pre-reproductive moult when the conspicuous glands were easily detected by casual inspection of the abdomen. Glair glands appeared to degenerate upon the completion of spawning as none were noted in females with freshly extruded eggs and old spermatophores collected in March-April.

Mating and spawning occurred from late February to early April in both 1986 and 1987 when mature males and reproductive females were found in the same burrows (Normally only one adult is found in each burrow system, see Chapter 7, section 7.3.1). In 1986 mating pairs were found from March 12 to April 10 while in 1987 they occurred from February 27 to April 3. Overall 2 pairs were found in February, 19 in March and 2 in April. Most pairing occurred in early March just prior to moulting in reproducing females (see Chapter 8). In March, 75% of reproducing females captured were paired in mid month and by the beginning of April all reproductive females (which had not spawned yet) were paired. Mating and spawning took place within one month of pairing. The earliest newly spawned female was collected on March 27, 1987 at which time only 20% of reproductive females had spawned. By April 3, 83.3% of reproductive females had spawned and by the middle of the month all previously reproductive females were in berry. These freshly spawned females all had the remains of spermatophores (or sperm plugs - see Fig. 7.4B) attached to their thoracic sterna, attesting to recent copulation.

Eggs were carried through the winter. Early embryonic development was first noted in eggs of females collected in August. In September the embryos were in late nauplius stage, by October their development progressed into the late protozoa stage. Hatching occurred in late November when females carrying eggs with fully developed embryos and/or early stage 1 young were captured (Fig 6.13). The young remained in this stage until mid December when they moulted to stage 2 (on Dec.17-19, 1986,

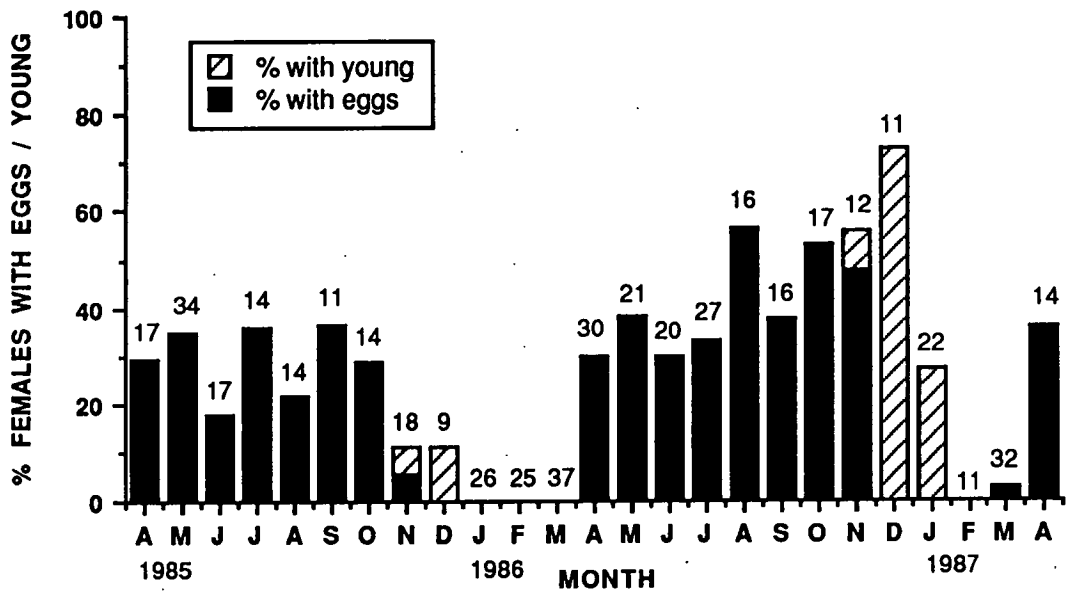


Figure 6.13 The percentage of *P.t. tasmanicus* females with eggs or young (stages 1-3) captured at Harlequin Hill from April 1985 to April 1987. (numeral on top of columns indicates number of mature females in monthly samples).

37.5% of females carried stage 1 young, 12.5% carried mixed stage 1-2 broods and 50% carried stage 2 broods). Stage 2 larvae were carried until early to late January when they moulted to stage 3 and became independent of their mothers (stage 3 young did not remain attached to their mothers as in *Astacopsis* (see Chapter 7, section 6.3.3). Free stage 3 young were found in burrows from mid December in 1985-86 and from mid January in 1986-87. The broods of juveniles remained in their mothers' burrow systems until just before she spawned again, approximately one year from their release. These young appear to stay at close proximity to their mothers as they are often collected from the same terminal chamber of the burrow. Broods were collected in the same burrows as (reproductive) females throughout the year and the young dispersed from their mother's burrow, only just before pairing for the next mating season occurred, at approximately one year of age and CPL 8-12 mm (see Chapter 8).

In laboratory mating pairs, copulation and spawning occurred from late March to mid April. The development of eggs and young of the broods of 27 females collected at various times of the year (Apr. to Dec.) were monitored in the laboratory at seasonal temperatures, 10 and 15°C. At seasonal air temperatures (10-16°C), eggs hatched from September to November. Eggs of females captured in May and June took 100 days to hatch while those of females captured in September took 45 to 57 days. At temperatures ranging from 15 to 18°C stage 1 lasted 15.3 days (s.d. = 2.0, range = 13 - 20, n = 12) and stage 2 required 37.5 days (s.d. = 4.5, range = 32 - 46, n = 12). At 15°C, eggs hatched from August to December with the date of hatching being dependent on date of capture (eggs from females captured in June to July took 50 to 70 days to hatch while those of females captured in December only took 8 days). Stage 1 took 14.9 days (s.d. = 1.8, range = 13 - 18, n = 7) and stage 2 required 41.6 days (s.d. = 4.7, range = 34 - 46, n = 7). At 10°C, eggs hatched from October to January with the date of hatching being dependent on date of capture (eggs from females captured in June and July took 101 to 115 days to hatch while those of females captured in December only took 5 to 13 days). Juvenile stages took a considerably longer period to develop with stage 1 lasting 35.9 days (s.d. = 2.2, range = 31 - 38, n = 8) and stage 2 requiring 71.0 days (s.d. = 6.2, range = 61 - 75, n = 8).

As in *Astacopsis*, mature females of this species of *Parastacoides* bred biennially. The representative female reproductive cycle is shown in Figure 6.14.

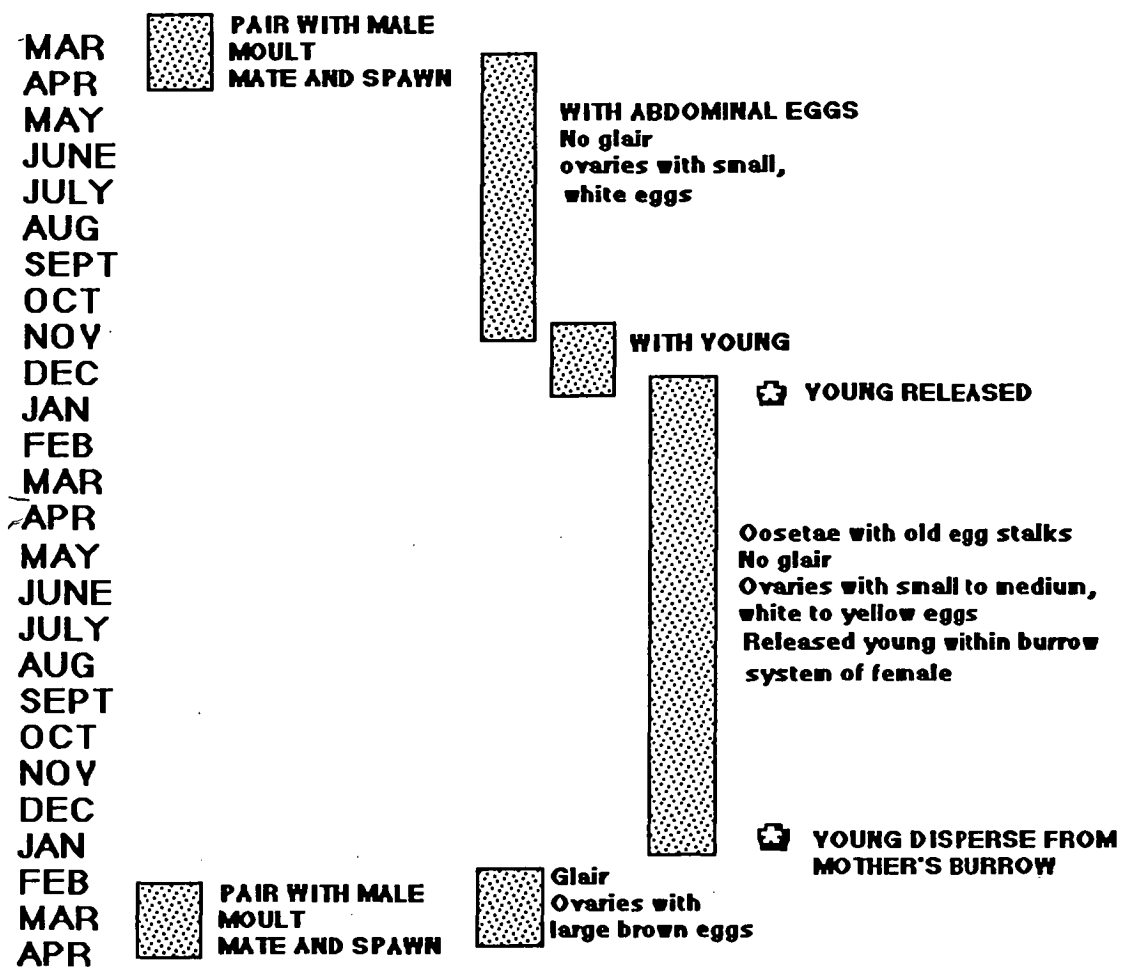


Figure 6.14 The typical biennial reproductive cycle of mature *P. t. tasmanicus* females from Harlequin Hill, South-West Tasmania.

Each breeding season only approximately 50% of mature females spawned in the Harlequin Hill population. In the 1985 - 86 season, 58.1 % of mature females were noted as reproductive and similarly in 1986 - 87, 53.5% were reproductive (n total = 350). Females which bred in 1985-86 did not breed in 1986-87 and conversely those which did not breed in 1985-86 bred in 1986-87. When the numbers of females in these two breeding groups was examined they showed an exact 50/50 ratio (175 females in each group).

Reproductive and nonreproductive females were present in all samples throughout the duration of the study. There was no difference in size between the breeding and nonbreeding groups ($t = 0.766$, $df = 234$, $p < 0.445$). The mean CPL of females which spawned in 1986 -87 was 30.5 mm (s.d. = 2.0, range = 23.6 - 36, $n = 112$) while that of females which did not breed was 30.3 mm (s.d. = 2.1, range = 25.6 - 35.2, $n = 124$).

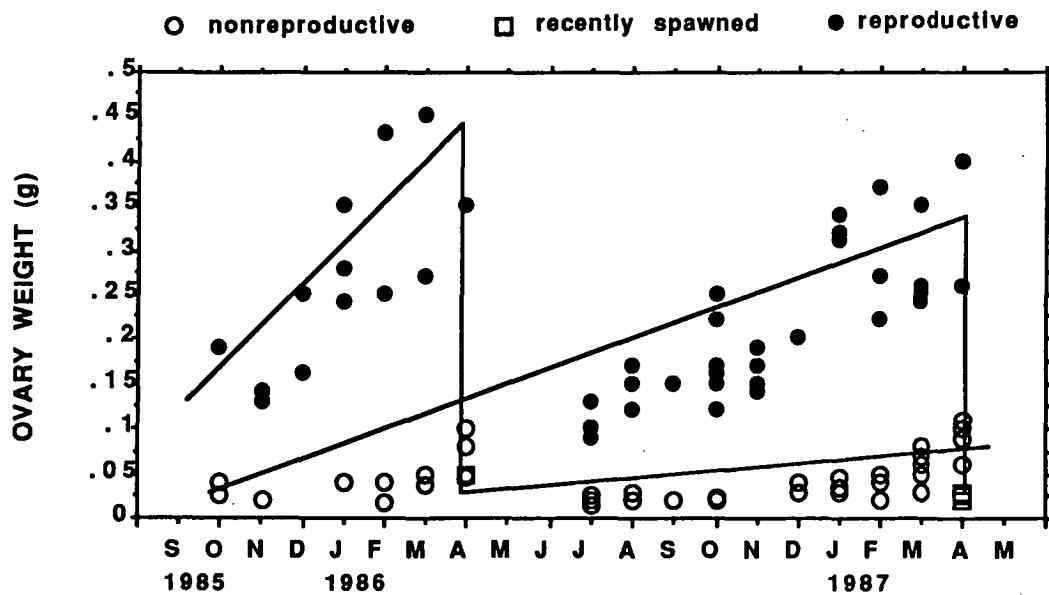
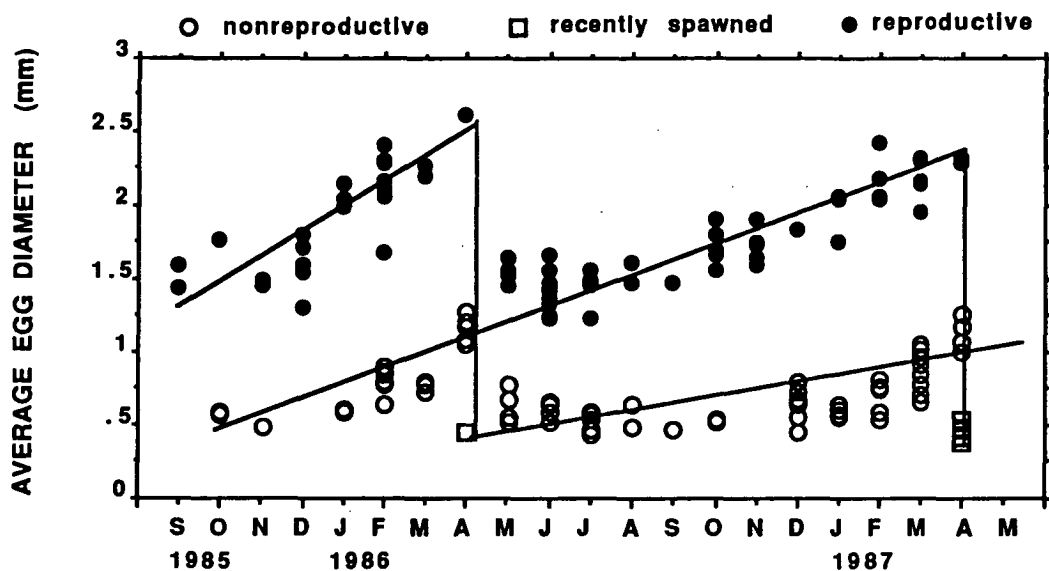
During and prior to the mating season, nonreproductive females were characterized by the lack of glair glands, small-to-medium, white-to-yellow ovaries (Fig. 6.8B3), the presence of eggs stalks on pleopods (Fig. 5.20b) and the occurrence of young of the year broods in their burrow systems. In contrast, reproductive females had well developed glair glands, large brown ovaries (Fig. 6.8B1), clean exoskeletons (ie: recently moulted) and long clean oosetae on pleopods (Fig. 5.20a).

The ovarian cycle of mature *P. t. tasmanicus* at Harlequin Hill is summarized in Figure 6.8B. The average ovarian egg diameter as well as ovary weight were significantly greater in reproductive females than in nonreproductive females throughout the year (egg diameter: $t = 19.2$, $df = 150$, $p < 0.0001$; ovary weight.: $t = 11.3$, $df = 105$, $p < 0.0001$). The resulting two female breeding groups could therefore be distinguished throughout the year by the stage of development of their ovaries (Figs. 6.15 & 6.16).

The biennial cycle was confirmed in the laboratory by long term observation of five females used initially for brood incubation experiments. The ovary development and moulting pattern of these females mirrored the cycle outlined in Figure 6.14. Multiple recaptures of three mature females in the pitfall traps also exhibited this cycle: in the best example, one female (CPL 33.7) was in berry in October 1985, with no brood and small white eggs in her ovary in April and July 1986 (ie: brood released), with medium yellow eggs in her ovary in May, September and October

Figure 6.15 Monthly growth of ovarian eggs in mature *P. t. tasmanicus* females preserved at Harlequin Hill from September 1985 to April 1987 (n total = 149). Females approaching spawning (reproductive) are represented by solid circles while those after spawning (nonreproductive) are shown as open symbols. Solid lines represent the approximate growth cycles of the ova in the two breeding groups (sharp declines indicate spawning).

Figure 6.16 Changes in ovarian weight in mature *P. t. tasmanicus* females preserved at Harlequin Hill from October 1985 to April 1987 (n total = 104). Females approaching spawning (reproductive) are represented by solid circles while those after spawning (nonreproductive) are shown as open symbols. Solid lines represent the approximate growth cycles of the ovary in the two breeding groups (sharp declines indicate spawning).



1986, with medium brown eggs in her ovary in January 1987 and with large brown eggs in her ovary and large gastroliths in March 1987 (i.e.: ready to moult and spawn again).

Abdominal eggs ranged from 2.4 to 3.0 mm in length and 1.8 to 2.3 mm in width (Fig. 6.17). The eggs of large berried females were only slightly larger than those of smaller ovigerous females (Fig. 6.18). When the average egg diameters of females $CPL \geq 30$ mm were compared to those of females $CPL \leq 29$ mm, the difference in egg size between the two groups was of only low significance ($t = 1.99$, d.f. = 51, $p < 0.05$). Abdominal eggs increased in both length and width during their lengthy incubation (Fig. 6.18). The eggs of berried females collected from April to June had a mean length of 2.63 mm (s.d. = 0.13) and a mean width of 1.96 mm (s.d. = 0.11) while those collected in October - November had a mean length of 2.78 mm (s.d. = 0.11) and a mean width of 2.15 mm (s.d. = 0.11). Although small, these seasonal differences in the eggs' dimensions were highly significant (length: $t = 3.97$, $df = 37$, $p < 0.004$; width: $t = 5.29$, $df = 37$, $p < 0.0001$).

The ovaries of immature females were smaller than those of mature females and contained small, generally yolkless ova (Fig. 6.19). The average egg diameter of immature females collected throughout the year ranged from 0.19 to 1.49 mm (mean = 1.48, s.d. = 0.41) with the diameter increasing gradually as females grew toward maturity (Fig. 6.19A). Some of larger immature females (CPL 24 - 30) were approaching maturity and their ovaries showed development of larger yolky ova as well as an overall increase in gonad size. Large mature females had proportionally heavier ovaries than smaller females ($t = 2.5$, $df = 23$, $p < 0.021$) but when the gonad weights were expressed as the percentage of total body weight no significant difference was found between large and small individuals ($t = 0.1$, $df = 18$, $p < 0.92$). Similarly although the average diameters of ovarian eggs in large females were larger overall, the difference between the two groups was not highly significant ($t = 1.66$, $df = 30$, $p < 0.11$).

The reproductive cycle of males was documented by determining the gonad condition throughout the year. As in *Astacopsis*, spermatophores consisted of coiled sperm tubes embedded in a clear matrix. During and prior to the mating season, spermatophores can be seen in the round and swollen vasa deferentia of mature males (Fig. 6.20C&D). The numerous spermatozoa seen within the sperm tubes are round, conspicuously nucleated and, as in *Astacopsis*, lacking rays. In contrast, the vasa

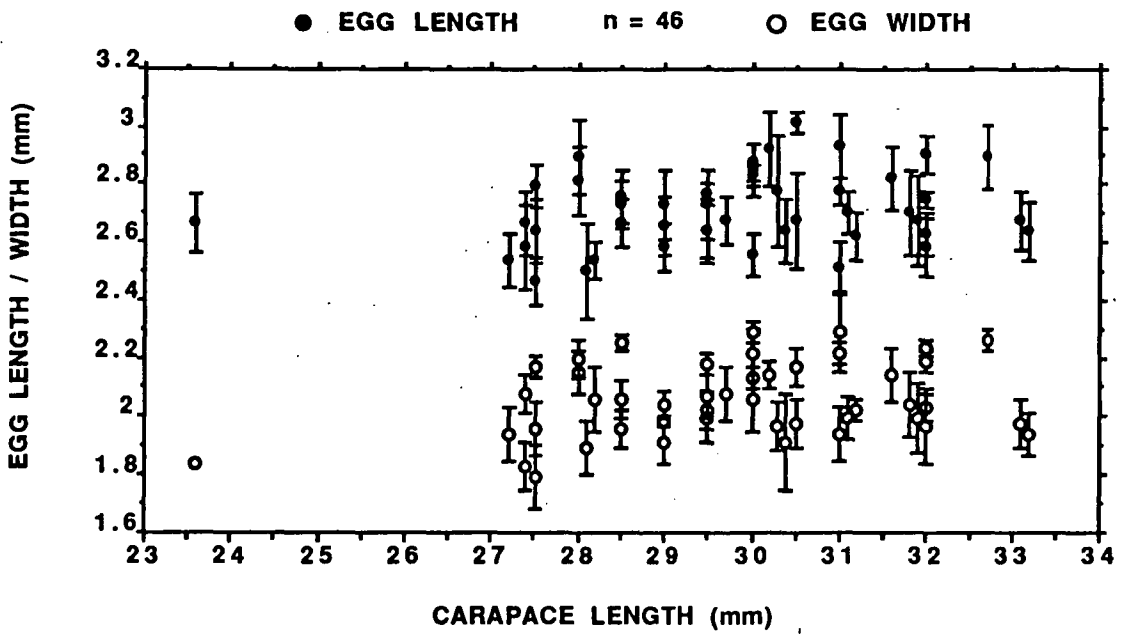


Figure 6.17 The relationship between carapace length and mean abdominal egg size (length and width) in berried *P. t. tasmanicus* females collected from April to November 1986 at Harlequin Hill.

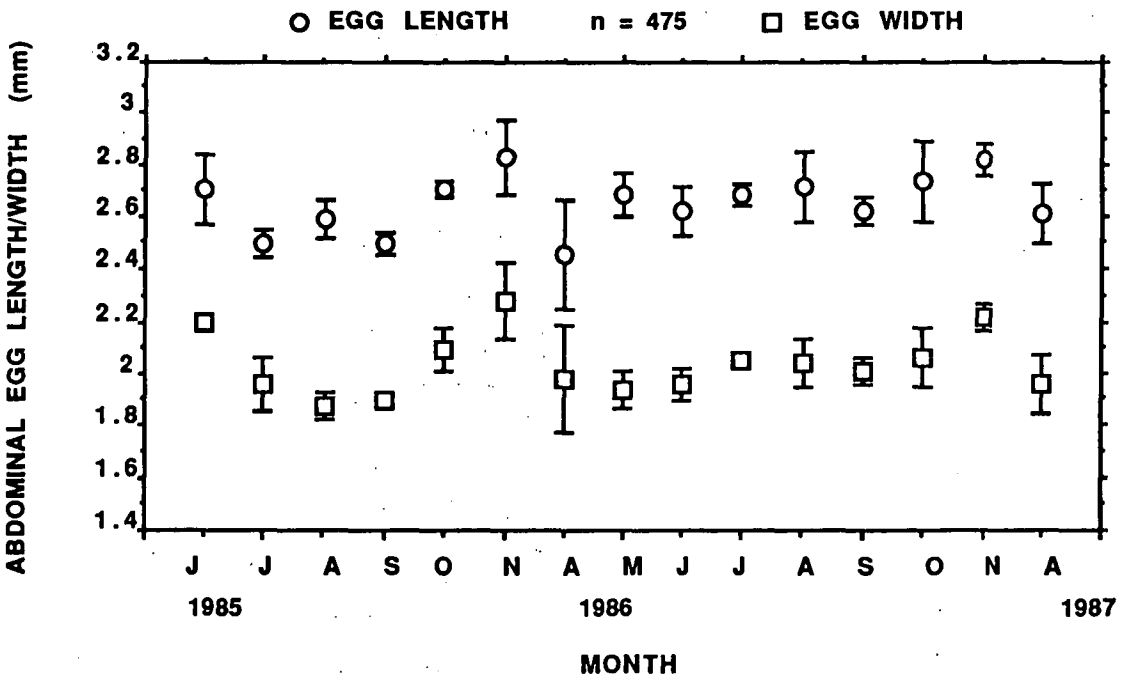


Figure 6.18 The growth of abdominal eggs (length and width) in berried *P. t. tasmanicus* females collected from June 1985 to April 1987 at Harlequin Hill (months when abdominal eggs are not carried are not shown).

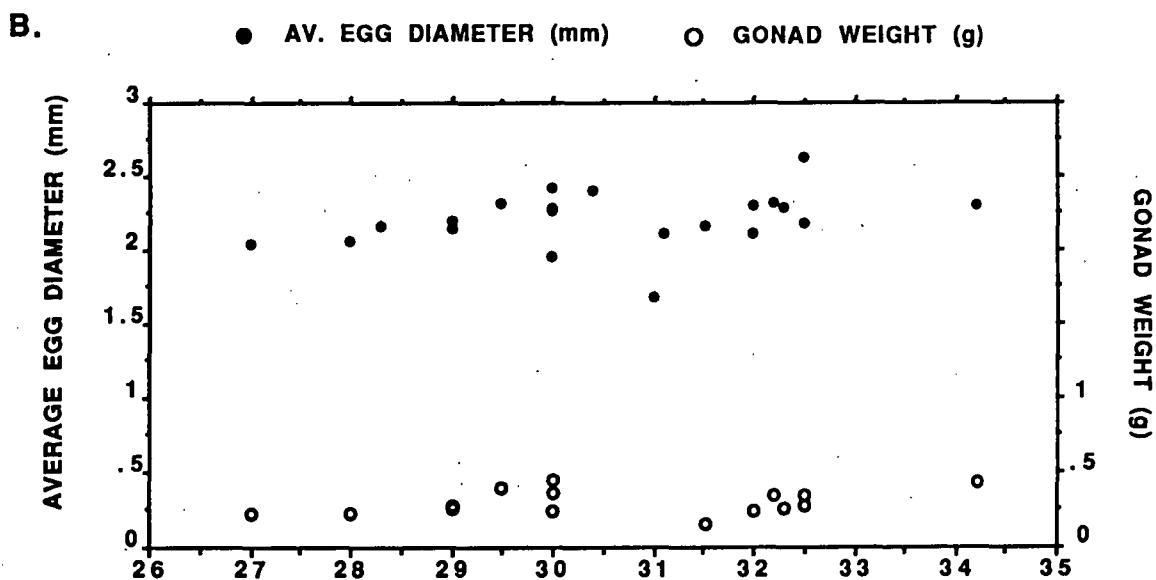
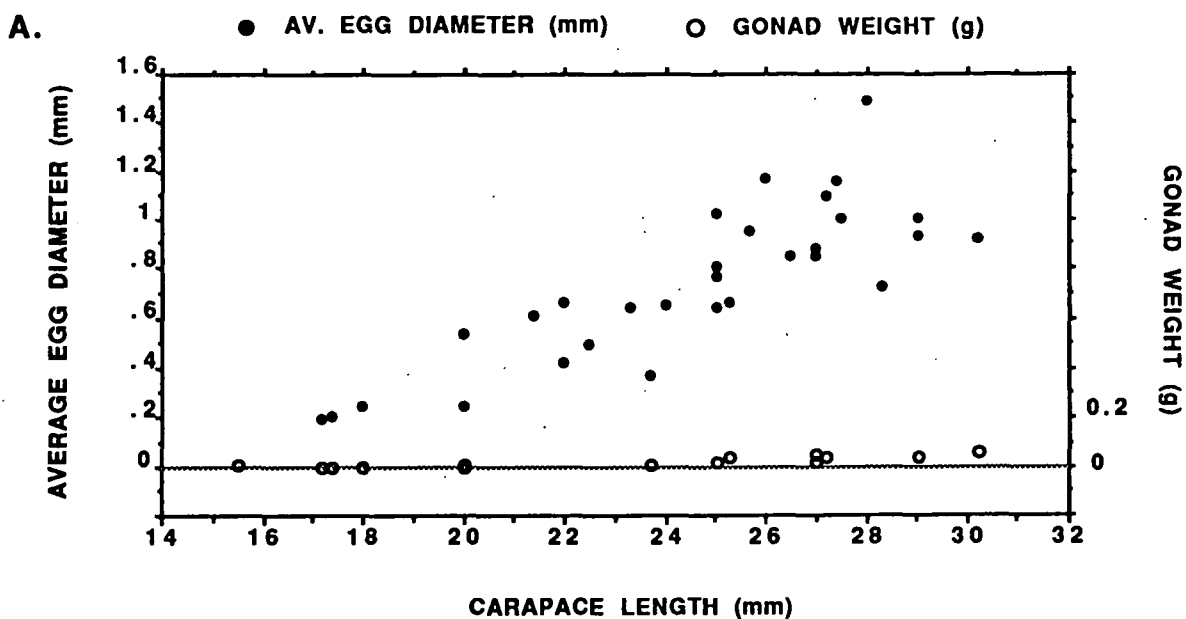


Figure 6.19 Average egg diameter and ovary weight of:

A. immature *P. t. tasmanicus* females from Harlequin Hill

(Feb. - Apr., n = 30);

B. mature reproductive *P. t. tasmanicus* females from Harlequin Hill

(Feb.-Apr., n = 22).

Figure 6.20 Cycling of male gonad anatomy in *P. t. tasmanicus* (SP):

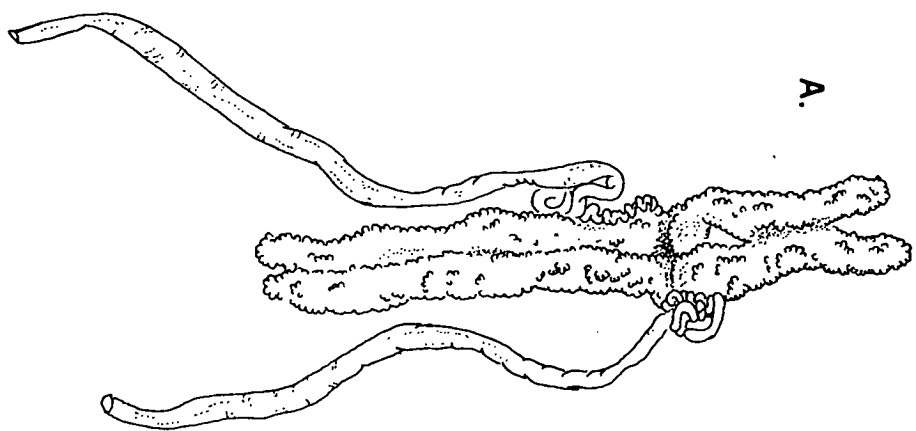
A. Testes and vasa deferentia of male CPL 29.0 mm. Captured 12.1.1987.

B. Cross section through vas deferens of gonad A. Note flattening of vas deferens and absence of sperm tubes.

C. Testes and vasa deferentia of male CPL 31.5.0 mm. Captured 13.3.1987 (paired with reproductive female).

D. Cross section through vas deferens of gonad A. Note roundness of vas deferens and presence spermatophoric mass (S) containing sperm tubes (St).

E. Detail of sperm tube



A.



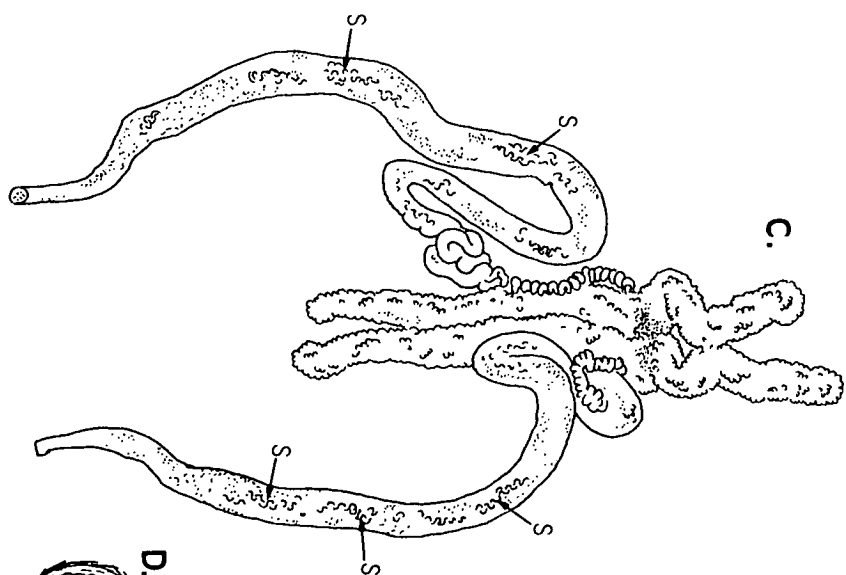
B.

1mm

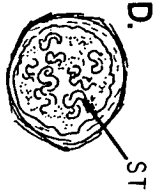
E

A C

B D



C.



D.



E.

deferentia of mature males collected in the spring were flattened, deflated and contained only a small amount of granular matrix (Fig. 6.20A&B). Sperm tubes began forming in late January, their number peaked in March - April, then, following the mating season, they began to break up, gradually degenerating through the winter (Figure 6.21). All mature males had reproductively functional gonads from mid February to early June, when sperm was detected within the unbroken tubes (Table 6.2).

The diameters of the vasa deferentia were smaller (the distal portions in particular) and the overall weight of the gonad were lower in mature males from spring to early summer but increased with the approach of the mating season (Fig. 6.22). The gonad weight was greatest in March (mean = 0.2 % of body wt., s.d. = 0.08) and lowest in November (mean = 0.074 % of body wt. s.d. = 0.002) while the mean diameter of the vasa deferentia was largest in April (mean = 0.80 mm, s.d. = .09) and smallest in January (mean = 0.62, s.d. = .001). The gonad weights and vasa deferentia diameters of males with spermatophores (February to May) were significantly larger than those without spermatophores (July to January), (vasa deferentia diameters: $t = 4.75$, d.f. = 95, $p < 0.0001$; Gonad weight: $t = 3.9$, d.f. = 65, $p < 0.0002$).

In reproductive males, vasa deferentia diameters increased with body size but gonad weights remained relatively constant. The largest vasa deferentia diameters were recorded in reproductive mature males of CPL 29 to 35 mm (Fig 6.23). The vasa deferentia diameters of mature males were significantly larger than those of immature males. In males preserved during and prior to the mating season the mean diameter of the vasa deferentia of mature individuals was 0.74 mm (s.d. = 0.12) while that of immature individuals was only 0.34 (s.d. = 0.18) : $t = 9.79$, d.f. = 61, $p < 0.0004$. The gonads of immature individuals were also much smaller but no quantitative assessment of the difference could be made because only few of the very small gonads could be dissected without some loss of tissue.

In summary, mature females of *P. t. tasmanicus* (SP) pair with males in their burrows, moult then mate and spawn in early autumn (March to early April), carry their eggs and young until well into the following summer (December to January), release their broods, overwinter, then mate and spawn again the following autumn, two years after their previous mating. This biennial breeding pattern results in two distinct female reproductive groups: reproductive and nonreproductive. The two

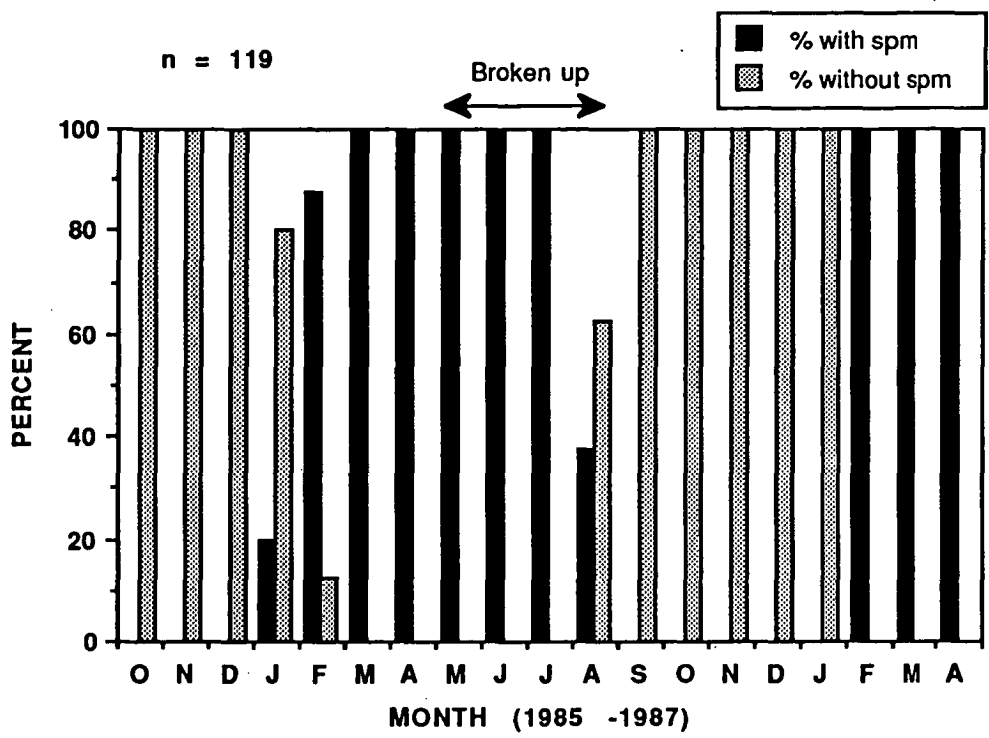


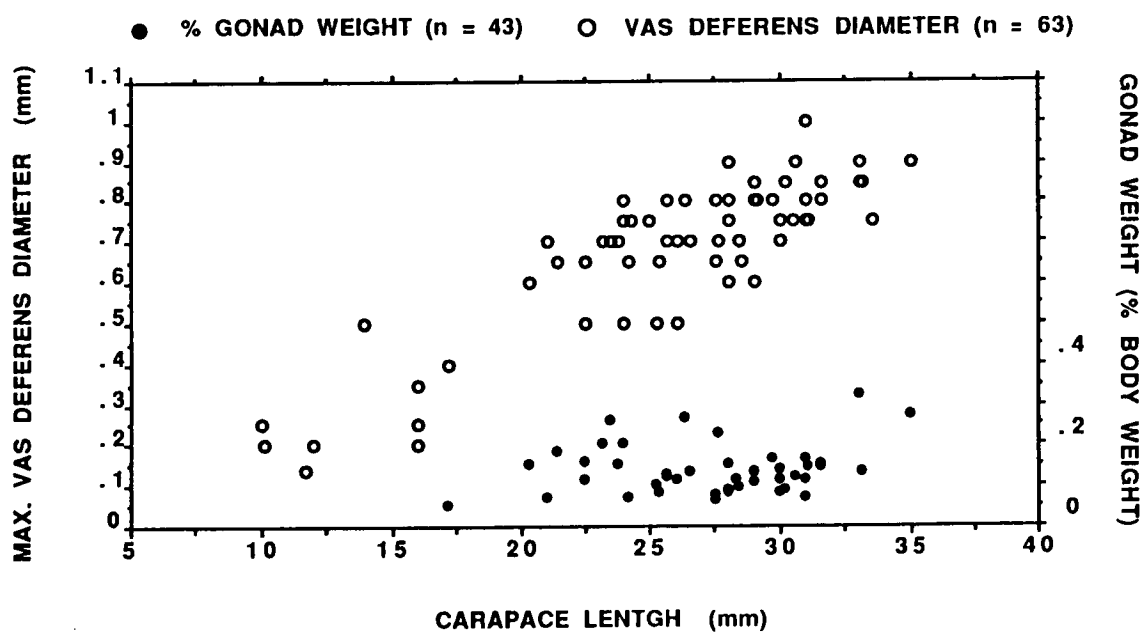
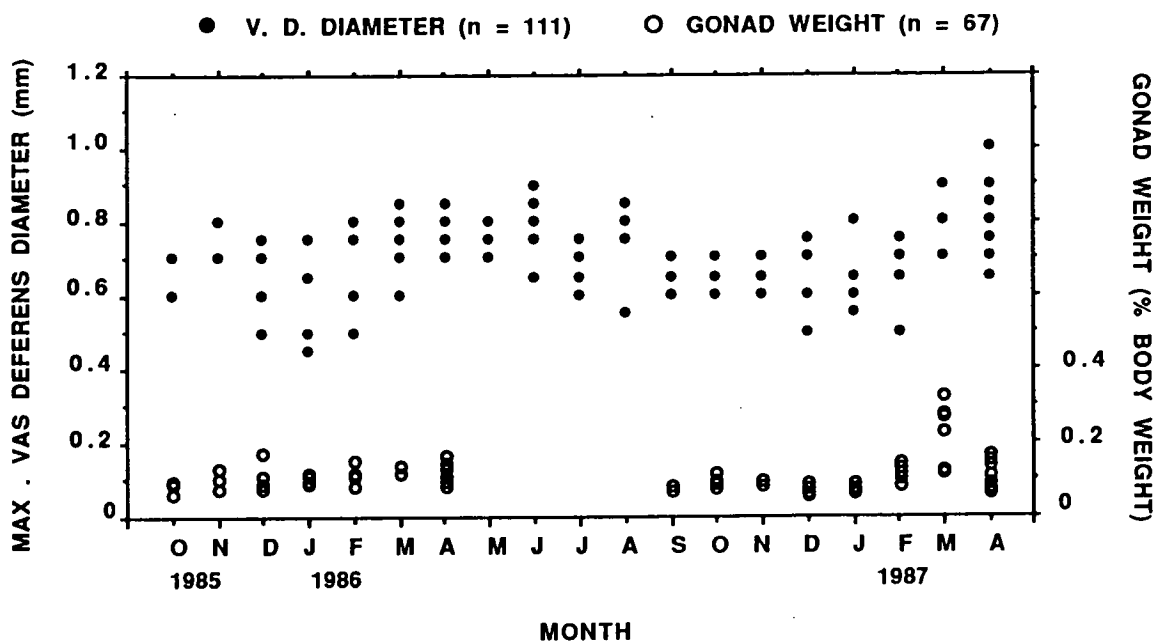
Figure 6.21 Percentage of mature *P. t. tasmanicus* males with spermatophores within their vasa deferentia in preserved samples from Harlequin Hill (October 1985 to April 1987).

Table 6.2. Spermatophore development in the yearly reproductive cycle of male *Parastacoides t. tasmanicus* from Harlequin Hill.

SEPTEMBER.....	Vas deferens flat and empty.
OCTOBER	No matrix, no sperm tubes.
NOVEMBER	
DECEMBER	
JANUARY.....	Vas deferens flat, generally empty with some matrix (in top coils mainly). No sperm tubes
FEBRUARY.....	Vas deferens rounder, fuller, with more matrix. Spermatophores low to moderate in number. Sperm within.
MARCH.....	Vas deferens round, very full.
APRIL	Matrix abundant. Sperm tubes numerous with sperm within.
MAY.....	Vas deferens round but less full. Sperm tube number low with sperm within.
JUNE.....	Vas deferens less full and flatter. Sperm tubes beginning to break up. Sperm low in number where present.
JULY.....	Vas deferens flat and mainly empty. Little matrix.
AUGUST	Sperm tubes broken up. No sperm.

Figure 6.22 Monthly variation in the maximum diameter of the vasa deferentia and gonad weight (expressed as the percentage of total body weight) in mature *P. t. tasmanicus* males from Harlequin Hill (October 1985 to April 1987).

Figure 6.23 The relationship between carapace length, maximum diameter of the vasa deferentia and gonad weight (expressed as the percentage of total body weight) in mature and immature *P. t. tasmanicus* males from Harlequin Hill (collected from February to April, 1986 & 1987).



groups can be easily separated on the basis of ovary development, presence of eggs or young and condition of secondary sexual characters. The gonads of reproducing females and males show synchronous cyclic development with peak development occurring just prior to the mating season. Larger females have the largest gonads and carry larger abdominal eggs than smaller mature females while larger males have proportionally larger vasa deferentia than their smaller counterparts. Abdominal eggs increase in size during the period of incubation. The rate of development of eggs and young is directly influenced by water temperature with higher temperatures causing accelerated development.

E. Other *Parastacoides* forms:

1. *P. t. inermis*: Limited information was collected throughout the year from the Harlequin Hill site. Females carrying eggs were collected from June to November. Eggs were in early development in June and advanced development (fully formed embryos) in November. Stage 1 and 2 young were attached to females in January and freelifving stage 3 young were found at this time.

Mating and spawning probably occurred between autumn and spring as some females collected in June 1986 still had large ripe ovaries. Males collected at this time had abundant sperm in their vasa deferentia and one of the three berried females captured had the remains of an eroded spermatophore attached to her sternum. One female with a ripe ovary was kept in the laboratory together with a male and subsequently mated and spawned the following spring.

Reproductive and nonreproductive mature females were found throughout the year suggesting a biennial reproductive cycle. Ovarian development was not monitored through dissections but reproductive females with large ovaries were noted in the field from January to June.

Abdominal eggs were smaller than those of *P. t. tasmanicus* (SP) ranging from 1.99 to 2.49 mm in length and from 1.68 to 2.04 mm in width. The development of eggs and young in the broods of 3 females collected on October 24, 1985 were monitored in the laboratory at seasonal air temperatures. Eggs hatched in December after 45 days at a water temperature of 12.5 to 17.5°C. Stage 1 young lasted 15 days (s.d. = 0) and stage 2 required 37.6 days (s.d. = 2.8, range = 36 - 41).

Males dissected in October had no sperm in their vasa deferentia and were preparing to moult.

Overall the reproductive cycle was generally similar to that of *P. t. tasmanicus* (SP) but spawning and mating may be prolonged from autumn to spring.

2. *P. t. insignis*: Limited information was collected from samples taken in October 1985 and 1986 from the Scotts Peak Dam site. Females carrying eggs at this time were in the same developmental stage as those of *P. t. tasmanicus* (SP) in October.

Reproductive and nonreproductive mature females were found in the samples suggesting a biennial reproductive cycle.

Abdominal eggs were intermediate in size between those of *P. t. tasmanicus* (SP) and *P. t. inermis*, ranging from 2.3 to 2.53 mm in length and from 1.96 to 2.06 mm in width. The development of eggs and young in the brood of one female collected on October 24, 1985 was monitored in the laboratory at seasonal air temperatures. Eggs hatched in late November after 36 days at a water temperature of 12.5 to 17.5°C. Stage 1 young lasted 20 days, stage 2 required 46 days and stage 3 young became independent immediately following the moult from stage 2.

Males dissected in October had no sperm in their vasa deferentia and were preparing to moult.

3. *P. t. tasmanicus* (N): Limited information was collected from samples taken in October 1985, 1987 and March 1988 from the Needles Range site. Females carrying stage 1 and 2 young were collected both in October and March. Freelifving stage 3 young were found in female's burrows in October.

Mating and spawning probably occurs in spring as all reproductive females collected in October still had large, ripe ovaries and soft and clean carapaces (evidence of very recent moult). In addition 50% of these females were paired with mature males in their burrows. Males collected at this time had abundant sperm in their vasa deferentia.

Reproductive and nonreproductive mature females were found in all samples suggesting a biennial breeding cycle. Overall 48.4% were reproductive and 51.6 % nonreproductive (n = 31). Ovarian development was not monitored through dissections but reproductive females had less developed ovaries in March than in October.

All mature males collected in October were in breeding condition (with sperm) while those captured in March appeared to be nonbreeding and preparing for a moult (all adult males had medium to large gastroliths).

The reproductive cycle was generally similar to that of *P. t. tasmanicus* (SP) but the timing of spawning, mating and moulting was significantly different. Mating and spawning probably occurs from spring to summer, eggs and young are carried through the summer with some broods staying attached until the following spring. Reproduction in this species appears to be, overall, less synchronous than in *P. t. tasmanicus* (SP).

6.3.3 Fecundity

A. *Astacopsis gouldi*

The number of abdominal eggs was positively correlated to carapace length (Fig 6.24). The smallest number of abdominal eggs carried was 244 on a female of 119 mm CPL, while the largest was 1300 on a female measuring 156 mm CPL. The mean number of eggs carried per female was 629.9 (s.d. = 359.7, n = 8).

The largest portion of a brood was attached to the second and third pair of pleopods while smallest was attached to the first pair (Table 6.3).

B. *Astacopsis franklinii* (Eastern form)

The number of abdominal eggs as well as young was positively correlated to carapace length (Fig 6.25) and the number of young was significantly lower than that of eggs suggesting some mortality occurs during development. The smallest number of abdominal eggs carried was 35 on a female of 41.8 mm CPL, while the largest was 118 on a female measuring 52 mm CPL. The mean number of eggs carried per female was 72.1 (s.d. = 22.7, n = 8). The number of ovarian eggs was not correlated to carapace length (Fig 6.25). The number of ovarian eggs is higher initially in early development (mean egg number = 114.9, s.d. = 73.0, range = 43 - 279, n = 8) but decreases as the ovaries ripen and ova increase in size (mean egg number = 74.7, s.d. = 20.9, range = 50 - 116 n = 18).

The largest portion of a brood was attached to the third pair of pleopods while smallest was attached to the first pair (Table 6.3).

C. *Parastacoides t. tasmanicus* (SP)

The number of abdominal eggs as well as young showed only a weak positive

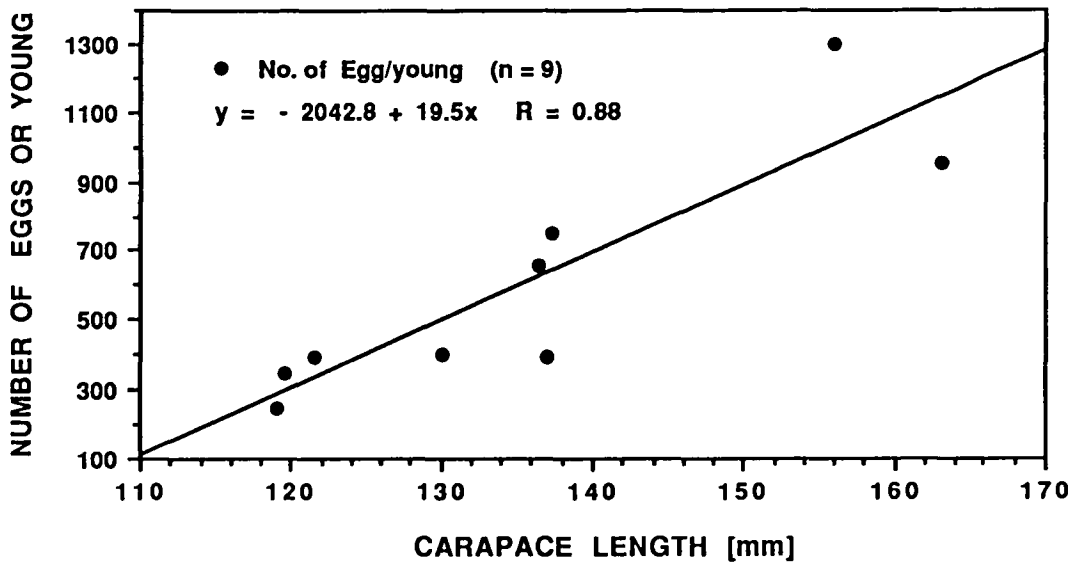


Figure 6.24 The relationship between carapace length and number of young, abdominal eggs and ovarian eggs in *A.gouldi* from various sampling sites.

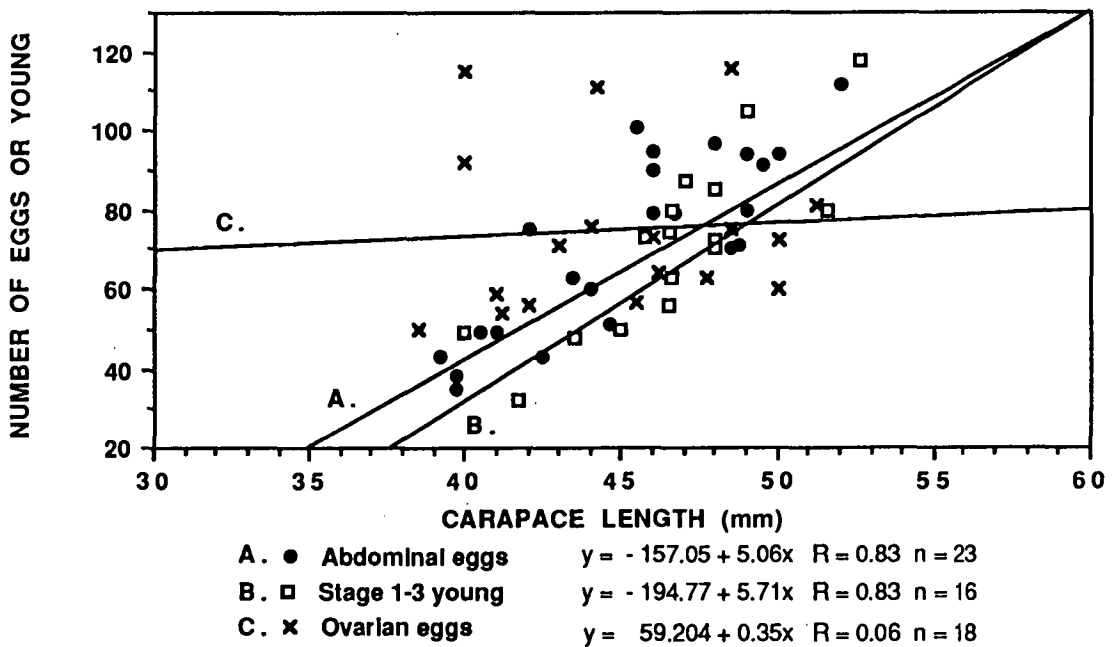


Figure 6.25 The relationship between carapace length and number of young, abdominal eggs and ovarian eggs in *A.franklinii* from Mt. Wellington streams

Table 6.3 Distribution of eggs in relation to pleopod pair in *Astacopsis gouldi*, *Astacopsis franklinii* (Eastern form) and *Parastacoides t. tasmanicus* (SP). Numbers are given as mean percentages of total number of eggs in brood. Number in parentheses is the standard deviation from the mean.

A.gouldi n = 5 broods

First pair	Second pair	Third pair	Fourth pair
22.0 (13.1)	28.4 (2.5)	28.4 (2.5)	27.0 (4.4)

A.franklinii n = 11 broods

First pair	Second pair	Third pair	Fourth pair
14.5 (3.6)	26.4 (4.3)	29.3 (4.0)	26.4 (4.0)

P. t. tasmanicus n = 15 broods

First pair	Second pair	Third pair	Fourth pair
19.3 (5.5)	26.0 (3.8)	26.5 (5.1)	28.2 (6.3)

correlation to carapace length (Fig 6.26) and the number of young was only somewhat lower than that of eggs. The smallest number of abdominal eggs carried was 23 on a female of 23.6 mm CPL, while the largest was 85 on a female measuring 32.2 mm CPL. The mean number of eggs carried per female was 55.7 (s.d. = 11.4, n = 86). As in *Astacopsis* the number of ovarian eggs was not correlated to carapace length (Fig 6.26). The number of ovarian eggs is higher initially in early development (mean egg number = 69.8, s.d. = 19.3, range = 40 - 105 n = 36) but decreases as the ovaries ripen and ova increase in size (mean egg number = 58.1, s.d. = 12.7, range = 42 - 88 n = 18).

The largest portion of a brood was attached to the fourth pair of pleopods while smallest was attached to the first pair (Table 6.3).

D. Other *Parastacoides* forms

Only limited data was collected for *P. t. inermis*, *P. t. insignis* and *P. t. tasmanicus* (N). The number of abdominal eggs as well as young was positively correlated with carapace length in all three "subspecies" (Fig 6.27). The broods carried by *P. t. inermis* were smaller than those of *P. t. tasmanicus* (SP) (mean egg number = 28.9, s.d. = 11.9, range = 13 - 49 n = 9), while the numbers of eggs carried by *P. t. insignis* and *P. t. tasmanicus* (N) were comparable to those of *P. t. tasmanicus* (SP) (mean egg number = 47.1, s.d. = 14.2, range = 22 - 62, n = 12). The small broods of *P. t. inermis* were mainly the result of the overall smaller size range of berried females in this "subspecies" (CPL range = 13 - 26 mm) when compared to the other three "subspecies" (Figs. 6.26 & 6.27).

6.4 DISCUSSION

Maturity size

A. gouldi females attain sexual maturity at carapace length (CPL) of 119 mm while males become physiologically capable of reproducing at a much smaller size of 76 mm CPL. This agrees with fishermen's reports of females greater than 4.5 inches (118 mm) CPL carrying broods (Lynch, 1967). Maturity in *A. gouldi* is reached at very large size and old age (see Chapter 8) when compared to most other freshwater crayfishes including the large spiny mainland Australian crayfishes in the genus

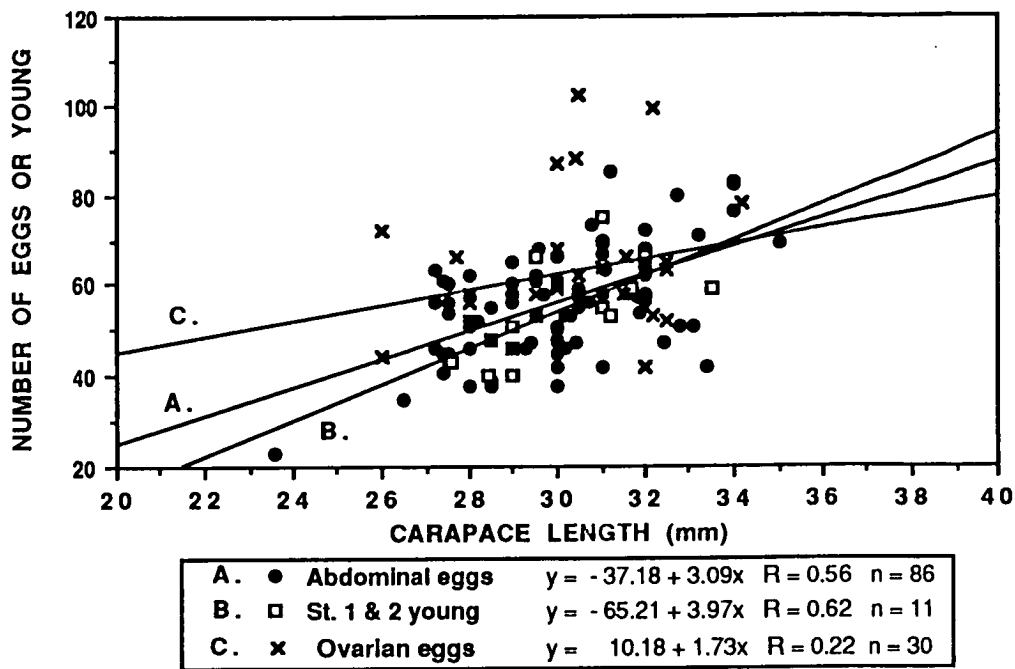


Figure 6.26 The relationship between carapace length and number of young, abdominal eggs and ovarian eggs in *P. t. tasmanicus* Harlequin Hill.

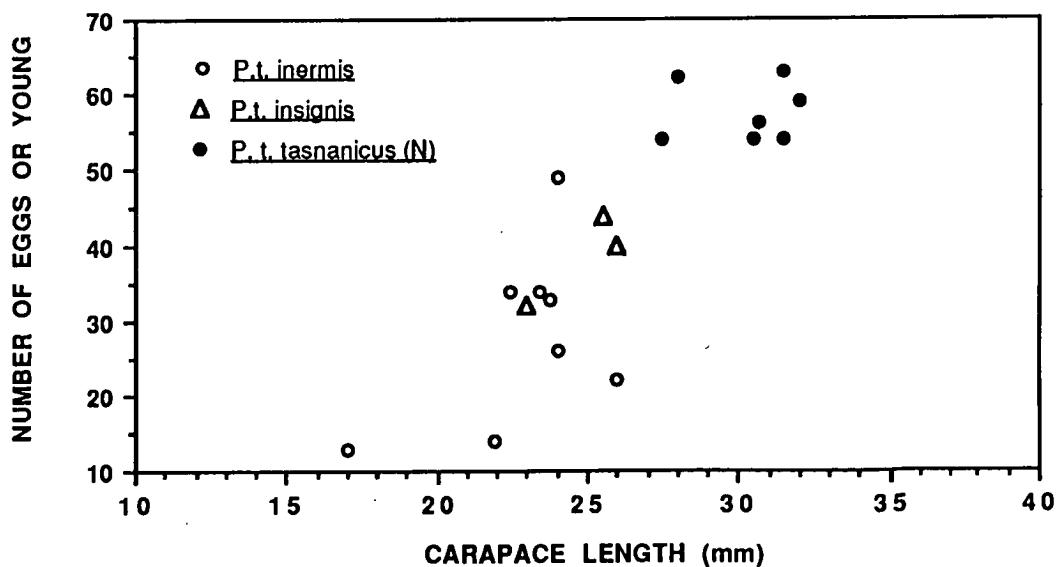


Figure 6.27 The relationship between carapace length and number of young / abdominal eggs in *P. t. inermis*, *P. t. insignis* and *P. t. tasmanicus* (N) from South West Tasmania.

Euastacus. Morgan (1986 & 1987), using gonopore morphology as an indicator, estimated female size of maturity to be between 51 and 126 mm CPL in *E. armatus*, between 62 and 111 mm CPL in *E. kershawi*, 72 mm CPL in *E. bispinosus*, 67 to 90 mm in *E. fleckeri* and 75 mm CPL in *E. hystricosus*. Hoey (pers. comm. 1989) found the size of maturity varied between populations of *E. bispinosus* in south-western Victoria ranging between 70 and 100 mm CPL while Turvey (1980) found the range of female size of maturity in *E. spinifer* to be between 84 and 114 mm CPL. Morison (1989) found that 50 % of female *E. armatus* in northern Victoria are mature at approximately 116 mm CPL. Large size at maturity has been associated with higher latitudes, colder environments and cool water temperatures (Aiken & Waddy, 1980; Momot, 1984) which are all characteristics attributable to *A. gouldi* distribution and habitats. There appeared little variation in size of maturity in the populations of *A. gouldi* sampled but the sites sampled all had similar habitat and environmental conditions and it remains to be seen, therefore, whether size at maturity varies in different habitats such as the rivers of the drier, warmer north east of the island. *A. franklinii* Eastern form matured at a considerably smaller size (39 to 46 mm CPL in females and 29 to 38 mm in males) while *A. franklinii* Western form showed some variation between populations but its' size at maturity was always greater than that of the eastern form (size of female maturity: 62 to 101 mm CPL). This again may be related to the larger and cooler water bodies of western Tasmania this form inhabits. Further surveys of populations of all three species/forms are needed to establish firmly the amount of variation present.

Parastacoides t. tasmanicus (SP) matures at a smaller size than *Astacopsis*, with female size of maturity ranging from 23 to 30 mm CPL while males mature (physiologically) between 16 and 25 mm CPL. *P. t. tasmanicus* (N) and *P. t. insignis* mature at similar size to *P. t. tasmanicus* (SP) but the overall smaller *P. t. inermis* matures at a considerably smaller size (females: CPL \geq 17 mm). Geographical variation in size of maturity was not investigated in any of the above "subspecies". This smaller size of maturity is predictably comparable to other similar-sized Tasmanian burrowing crayfishes: Suter (1977) found the size of maturity in females of *Engaeus fossor* and *E. cisternarius* ranged between 21 and 25 mm CPL while Horwitz (1986) found the minimum size at maturity of females in various species of *Engaeus* to be between 11 and 25 mm CPL.

Maturity in the *Parastacoides* and *Astacopsis* populations sampled is therefore

attained over a considerable size range in both sexes with 100% maturity being attained in relatively large crayfish in each species. Variability in size of attainment of maturity is common among the Astacidea (Hopkins, 1967A; Johnson, 1979; Turvey, 1980; Aiken & Waddy, 1980; Brewis & Bowler, 1985; Hamr & Berrill, 1985; Woodlock & Reynolds, 1988) and may reflect different environmental conditions from season to season or variation in food consumption and growth rates in various individuals.

In both *Parastacoides* and *Astacopsis*, males became mature at a smaller size than females. This phenomenon has been reported in other Parastacidae (Woodland, 1967; Johnson, 1979; Turvey, 1980) and Nephropidae (Aiken & Waddy, 1980) while in the Cambaridae and Astacidae the size of maturity appears similar in males and females (Prins, 1968; Price & Payne, 1984; Hamr & Berrill, 1985; Woodlock & Reynolds, 1988B). Woodland (1967) suggested that males mature earlier because of the lower energy requirement to produce sperm, compared with that needed to produce oocytes. Turvey (1980) hypothesized that the difference may be accounted for by the greater cost of reproduction to females in terms of growth rate, assuming that females must be large to survive and reproduce successfully. Aiken and Waddy (1980) proposed that two aspects of male maturity must be considered: "physiological", where a male is capable of producing mature spermatozoa, and "functional", where a male is actually capable of courting and mating with a female. They point out that small mature lobsters are well below the smallest sizes of females at first maturity and may not be capable of mating with the larger females. This scenario is easily translatable to freshwater crayfish and it has been shown that small males are excluded from mating either by competition with larger males or by female sexual selection (Berrill & Arsenault, 1984; Woodlock & Reynolds 1988A). Indeed in the *P. t. tasmanicus* mating pairs collected during this study, most males were of large size (CPL ≥ 27 mm) and paired with females of equal or smaller size (see Chapter 7, section 7.3.1). Turvey (1980) found very small physiologically mature males in a population of *E. spinifer* which he termed "precocious". He established that these males were capable of mating with larger females in the laboratory and hypothesized that they may be opportunistic breeders, especially when numbers of larger males are reduced or their movement is inhibited by environmental conditions. He did not however establish the life span of these males to ascertain whether they die at smaller size than normal males or continue to grow to a normal adult size and thus

gain a considerable advantage by being able to breed at a very small size.

The criteria used for establishment of maturity in this study were the presence of abdominal eggs and secondary sexual characters as well as ovary condition in females and the presence of spermatophoric material within the vasa deferentia of males. Female secondary sexual characters such as gonopore setation, cement glands, widened abdominal segments and oostetae are useful indicators of maturity and some have been used in several studies of crayfishes and lobster species (Morrissey, 1970; Turvey, 1980; Aiken & Waddy, 1980; Morgan, 1986 & 1987). The decalcification of the tail fan in *Astacopsis* was demonstrated as an additional previously undescribed character. This study also demonstrates that because each character is acquired independently and gradually prior to the attainment of maturity, only females with the entire complement of fully developed sexual characters should be considered as sexually mature. Male maturity can be reliably established only through dissection of gonads just prior to and during the reproductive season as none of the external characters used for other species such as chela size (Aiken & Waddy, 1980) and genital papilla inflation (Turvey, 1980) can be used to clearly and accurately establish the onset of maturity in *Astacopsis* and *Parastacoides*.

Seasonal breeding cycle of mature animals

Adult females of *Astacopsis* and *Parastacoides* exhibit a biennial breeding and moulting cycle. This biennial breeding cycle is a life history strategy previously undocumented in the Parastacidae. It is unclear whether such a cycle occurs in other Tasmanian Parastacidae since there are no detailed long term studies of their life histories. Biennial breeding cycles have been observed in northern European populations of *Astacus astacus* where females produce clutches in alternate years so that in any given year fewer than half of the females produce eggs (Abrahamsson, 1973; Huner & Linquist, 1986; Pursiainen et. al., 1988). Similarly, females of the American and European lobsters of the genus *Homarus* exhibit a two year ovary maturation cycle, with mating and spawning occurring biennially (Aiken & Waddy, 1980). Fradd (1979) discounted Lake and Newcombe's (1975) low fertilization theory to explain the occurrence of nonreproducing adult females in *Parastacoides* and, in his study of the eco-physiology of *P. t. tasmanicus* and *P. t. insignis*, proposed that females bred only once every two years, basing his argument on the difference in ovary condition and annual variation in the organic composition of body

tissues of berried and nonberried females. He found that during the non-berried part of the cycle, energy stores in the midgut gland, in the form of lipids, increased in preparation for the pre-reproductive moult and at the same time the gonads increased in size and stage of development. In contrast, during the berried part of the cycle the energy stores in the hepatopancreas and other tissues remained low and gonads did not grow large. Similarly Huner and Linquist (1986) found the *Astacus* females which had produced young in the summer lacked sufficient energy reserves to both moult and replenish ovaries in the short period between release of young and the following autumn. These findings agree with the results of this study from which it is apparent that the ovaries of females which have just released young are much too small to produce mature ova again in autumn. These females apparently require an entire year to build up enough energy to develop their ovaries and to moult prior to spawning. In addition to the overall low nutrient availability in the environment, it is possible that the overall foraging activity is reduced in berried females in order to protect their broods. Females carrying broods would thus forage just enough to sustain themselves and not accumulate any significant energy reserves. The biennial breeding cycle therefore appears to be the result of the combination of cold temperatures and low nutrients in the crayfishes' environment. The yearly mean water temperatures are relatively low (9-12°C) with monthly lows seldom exceeding 10 °C (see Chapter 4). The adult diets of both *Astacopsis* and *Parastacoides* consist mainly of relatively low nutrient plant material (Gould, 1870; Lake & Newcombe, 1975; Grown & Richardson, 1988). Furthermore nutrient uptake is decreased by slower consumption and digestion rates during the winter months as is the overall nutrient availability, especially in the case of protein rich food (Fradd, 1979; Grown & Richardson, 1988).

The timing of mating, spawning and egg/larval incubation was similar in *A. gouldi* and *A. franklinii* but differed significantly in *P. t. tasmanicus*. Females of *Astacopsis* mate and spawn in autumn (April-May) and carry eggs over winter, young hatch in January and may remain attached until well into the following autumn (March-May). In *Parastacoides*, females pair, mate and spawn in autumn (March-early April), carry eggs over winter, young hatch in late November and may remain attached until mid summer (December-January). Incubation of eggs and young was longer than in any other parastacid taking 10 to 12 months in *Astacopsis* and 9 to 10 months in *Parastacoides*. In previous studies of the two genera Lake and Newcombe

(1975) found that *P.t. tasmanicus* (SP) females carried eggs from April to November and young remained attached until February-March. The longer period of larval incubation was likely due to cooler water temperatures at the time of their study. Forteath (1985) proposed, on the basis of undocumented field observations, that most female *A.gouldi* extruded eggs in April-May and carried young until February. He further proposed that some females may also spawn in the spring and carry young into late summer. No evidence of spring spawning was found during this study as all berried females captured in the spring had well attached developing eggs. Autumn spawning and prolonged egg incubation (7-9 months) have been documented in several other parastacids: Turvey (1980) found that *Euastacus spinifer* in New South Wales mated and spawned in May-June, carried eggs to November and young until December; Hoey (pers. comm.1989) found that *Euastacus bispinosus* in Victoria spawned in early May, carried eggs until October-November and then young for approximately an additional month; Hopkins (1967A) found *Paranephrops planifrons* in New Zealand carried eggs from April to November and young until December. Other Parastacidae breed in the spring and incubate their young through the summer. *Engaeus cisternarius* carries eggs from October to February and young remain attached until April in northern Tasmania (Suter, 1977), while berried females of other Tasmanian *Engaeus* species were recorded in August and from November to January (Horwitz,1986).

In the genus *Cherax* the incubation period is shorter and multiple spawnings per summer may occur (Johnson, 1979). The widely distributed *C. destructor* begins mating and spawning in the spring (Sept.-Oct.), the incubation period lasts about three months and females with eggs and young can be found until March (Johnson,1979; Lake & Sokol, 1986). In the West Australian *C. tenuimanus*, mating occurs in September to October and broods are carried until November to January (Shipway ,1951; Morrissy, 1970). Similarly, in the Chilean parastacid *Samastacus spinifrons*, Bocic *et. al.* (1988) found that ovigerous females occurred from December to August with peak numbers in February-March and June-July, and speculated that its life cycle may be semiannual.

Most northern hemisphere crayfishes such as *Orconectes*, *Procambarus* and *Cambarus* have relatively short breeding seasons with mating in fall and early spring, spawning from spring to early summer and the incubation period lasting approximately 4-8 weeks (Crocker & Barr, 1968; Hamr & Berrill, 1985; Huner,

1988). Some cambarids and astacids such as *Orconectes immunis*, *Pacifastacus leniusculus*, *Austropotamobius pallipes*, *Astacus astacus* and *Astacus leptodactylus* have a longer breeding season, spawning in autumn and carrying eggs through the winter with an incubation period of 5-8 months (Crocker & Barr, 1968; Brewis & Bowler, 1985; Cukerzis, 1988; Köksal, 1988).

The onset of spawning in *Astacopsis* and *Parastacoides* is associated with decreasing water temperature and increasing water levels in autumn. Mating and spawning occurred in *A. gouldi*, *A. franklinii* and *P. t. tasmanicus* as water temperatures dropped permanently below 15°C, and this cycle was repeated in successive sampling seasons (see Chapter 4). Temperature has been demonstrated and cited as an important reproductive cue in several crayfish and lobster life cycles (Lowe, 1961; Aiken, 1969; Johnson, 1979; Aiken & Waddy, 1980; Berrill & Arsenault, 1982). An additional stimulus may be shortening daylength which has been shown to influence spawning in other freshwater crayfishes (Lowe, 1961; Aiken, 1969). The difference in timing of reproductive events between *Astacopsis* and *Parastacoides* may be due, therefore, to the differences in temperature between the habitats of the two genera. Overall *Parastacoides* experiences and tolerates warmer summer temperatures than *Astacopsis* which can significantly speed up ovary development as well as incubation of eggs and young. Water may reach high temperatures (25 to 30°C) in shallow burrows or the top passages of the burrow system and short term exposure to these temperatures may further speed up reproductive development. In contrast the water temperature in the swift flowing *Astacopsis* habitats stays relatively cool and constant.

The gonads of reproducing females and males in *Astacopsis* and *Parastacoides* show synchronous cyclic development with peak development and heaviest weights occurring just prior to the onset of the mating season. Vasa deferentia and ovarian egg diameters were greatest in April and May in *Astacopsis franklinii* and from March to April in *Parastacoides tasmanicus*.

Because of its biennial nature, the ovarian maturation cycle in *Astacopsis* and *Parastacoides* is unlike any other seasonal ovarian maturation described in the Parastacidae, Cambaridae or Astacidae (Lowe, 1951; Prins, 1968; Morrissy, 1970; Johnson, 1979). Ovaries develop very little during the first summer after spawning (while females are carrying broods) and development only begins once broods are released and females can actively forage and build up adequate energy supplies to

molt and produce the next brood. The amount of sperm in the vasa deferentia of mature males of both genera decreased following the mating season and the gonoducts were devoid of sperm from early winter (June) to late summer (January). Sperm began forming in February and by March was very abundant. Large males had the largest amounts of spermatophoric mass within their gonoducts and may therefore have a better chance of successfully fertilizing one or more reproducing females. There are only a few studies of the male reproductive cycle in freshwater crayfishes: Johnson (1979) found sperm in the vasa deferentia of *Cherax destructor* during all months except April, May and June; Woodlock and Reynolds (1988B) found the weight of vasa deferentia increased as males approached the mating season and noted a correlation between frequency of mating and decrease in vasa deferentia weight in *Austropotamobius pallipes*; Lahti and Linquist (1983) found the testes of *Astacus astacus* attained peak weight several months before copulation (June) while the vasa deferentia reached peak weight just before copulation (October).

The description of the formation of glair glands prior to mating, in this study, is the first report of this phenomenon in the Parastacidae. The strongest development of these glands coincides with ripening of the ovary and glands disappear soon after spawning. Previously glair glands have been shown to undergo cyclic development parallel to ovarian development in lobsters and some northern hemisphere crayfishes (Stephens, 1952; Aiken & Waddy, 1982; Hamr and Berrill, 1985). A detailed study of the cyclic development of glair glands in the Parastacidae is needed to show whether their glair glands show similar development throughout the year to that documented in other Astacidea.

The abdominal eggs of *Astacopsis* and *Parastacoides* were similar to those of other parastacids, being relatively large and ovoid (ie: elliptical). The eggs of *A. gouldi* were much larger than those of other crayfishes with a maximum length of 5.7 mm and a maximum width of 4.2 mm while eggs of *A. franklinii* were smaller, having a maximum length and a maximum width of 3.9 mm and 3.2 mm respectively. Similarly, the eggs of *Euastacus bispinosus* have a mean egg size of 4 by 2.9 mm, while in *E. spinifer* eggs had a length of 3.2 to 3.9 mm and a width of 2.4 to 2.9 mm (Turvey, 1980). The eggs of the large *Cherax tenuimanus* have a maximum length of about 4.0 mm (Morrissey, 1975). Eggs of *Parastacoides* were smaller than those of *Astacopsis* having a maximum length of 3.0 mm and a maximum width of 2.3 mm. This is comparable to the eggs of other burrowing crayfishes such as *C.*

destructor which have a length of 2.0 to 2.5 mm and a width of 1.5 to 2.0 mm (Johnson, 1979). In the Chilean genus *Parastacus*, *P. nicoletti* has a maximum egg diameter of 2.2-2.9 mm while in *P. pugnax* it is 2.6 to 2.84 mm (Rudolph & Zapata, 1986; Rudolph & Rios, 1987). The eggs of the Astacidae and Cambaridae are more round than those of the Parastacidae, ranging in diameter from 2.0 to 3.0 mm in *Astacus* (Cukerzis, 1988; Köksal, 1988) and 2.5 to 2.7 mm in *Cambarus* (Hamr & Berrill, 1985).

Although the development of young is abbreviated in *Parastacoides* (ie: stage 3 young are independent) the length of the postlarval incubation period is of similar duration as in *Astacopsis*. At 15°C, the total larval incubation period lasted 52.8 days in *P. t. tasmanicus* (SP) as well as in *A. gouldi* while in *A. franklinii* it took 44.5 days. The larval incubation period in other Australian parastacids varies in duration from relatively short in *Cherax destructor* (20 days) to long in *Engaeus cisternarius* (50 to 70 days) (Johnson, 1979; Suter, 1977). In the New Zealand species *Paranephrops planifrons* larval incubation is also long (more than 50 days), and the Chilean species *Parastacus nicoletti* has a long incubation of 69 days, while *P. pugnax* only requires 15 days from hatching to independence (Hopkins, 1967A; Rudolph & Zapata, 1986; Rudolph & Rios, 1987). Larval incubation in the Astacidae and Cambaridae is relatively short lasting from 10 to 23 days in *Cambarus* and *Orconectes* (Prins, 1968; Price & Payne, 1984; Hamr & Berrill, 1985) and 16 to 34 days in *Astacus* and *Pacifastacus* (Andrews, 1907; Köksal, 1988). Abbreviated development as seen in *Parastacoides* also occurs in *Parastacus*, *Pacifastacus* and *Astacus* (Andrews, 1907; Rudolph & Zapata, 1986; Rudolph & Rios, 1987; Köksal, 1988).

The rate of development of eggs and young is directly influenced by water temperature with higher temperatures causing accelerated development. In *P. t. tasmanicus* the incubation period was 1.9 times longer at 10°C than at 15°C. This further illustrates the major effect temperature fluctuations can have on growth and reproductive activity. For example, in 1985 at Harlequin Hill, independent stage 3 young were collected from shallow roadside burrows a full month earlier than in deeper cooler button grass burrows. It appears therefore that a given species' egg and larval incubation period is influenced by the general temperature trends within its habitat as well as year to year and microclimate variation in this temperature.

Lake and Newcombe (1975) stated that young of *P. t. tasmanicus* "fled" from

their mothers as soon as they became independent and left the maternal burrow system when water levels rose in autumn to early winter. The results of this study do not support this view as broods were found in the burrow systems of their mothers for up a year after they became independent (See also Chapter 8). Furthermore the young were at very close proximity to their mothers for several months after release. Such behavior has also been documented in the burrowing crayfish *Engaeus leptorhyncus* (Horwitz *et al* 1985). Long term laboratory observation of *P.t. tasmanicus* females and young showed that mothers were not aggressive toward their broods and no cannibalism was observed. The juveniles, although they generally avoided each other, showed little aggressive behaviour when compared with *Astacopsis* broods, where aggression, major injuries and cannibalism were common.


Fecundity

The number of abdominal eggs as well as young was positively correlated to carapace length in all species examined. This positive relationship between carapace length has been demonstrated in numerous members of the Astacidea (Hopkins, 1967A; Prins, 1968; Abrahamsson, 1971; Morrissy, 1970; Turvey, 1980; Aiken & Waddy, 1980; Hamr & Berrill, 1985; Brewis & Bowler, 1985; Bocic *et. al.*, 1988). The large *A. gouldi* has therefore the highest recorded potential fecundity of any freshwater crayfish, carrying broods of up to 1300 eggs. The large number of eggs in this species is probably offset by its very long life span during which mortality is inevitably high. The maximum number of abdominal eggs recorded in other large closely related parastacids was 1200 in *E. bispinosus* (Clark, 1937), 800 in *E. armatus* (Johnson, 1974) and 779 in *E. spinifer* (Turvey, 1980) while the largest of the remaining members of the family, *C. tenuimanus* has a maximum potential fecundity of 1200 (Morrissy, 1970). *A. franklinii* had a higher fecundity (range: 35 - 118) than the overall smaller *P. t. tasmanicus* (range: 23 - 85) while the smallest broods (as low as 13) were found on the smallest "subspecies" of *Parastacoides*, *P. t. inermis*. In the only other study available for comparison, Lake and Newcombe (1975) found the number of abdominal eggs ranged from 38 to 80 in *P. t. tasmanicus*.

The number of young was somewhat lower than that of eggs suggesting some mortality may occur during development. The small loss of eggs and young during the long period of incubation may be attributed to mechanical stress such as water flow

and abrasion against rocks in *Astacopsis* or dehydration, anoxia and abrasion against burrow walls in *Parastacoides*. Moulting in larvae can also contribute to the mortality of broods (see Chapter 7). The largest portion of a brood is attached to the second and third pair of pleopods in *Astacopsis* and to the fourth pair in *Parastacoides*, while the smallest portion is attached to the first pair in both genera. Similar egg distribution patterns were found in *P. t. tasmanicus* (Lake and Newcombe, 1975) and in *Paranephrops planifrons* (Hopkins, 1967A). This distribution pattern may be related to the shape of the abdomen and the brooding chamber formed by its terga and tail fan: abdominal segments are widest in the middle of the tail and the tail, when curled under, can not reach to cover and protect the first pair of pleopods (see Chapter 7). Loss of eggs from the first and last pairs of pleopods may also result from the movement of the female ie: articulation between abdomen and thorax and tail flipping.

The number of ovarian eggs was not correlated to carapace length in either *Astacopsis franklinii* or *Parastacoides tasmanicus*. The number of ovarian eggs is higher initially in early development when ova are small and yolkless, but decreases as the ovaries ripen and ova increase in size. The number of ova which ripen in a given season is probably determined by the energy obtained from available food resources and therefore is not dependent solely on a female's size. Since the diets of adult *Parastacoides* and *Astacopsis* are generally nutrient-poor (Gould, 1870; Fradd, 1979, Growns & Richardson, 1988) it can be expected that larger females may not necessarily have the highest energy stores allocated for reproduction, that is to say, where nutrients are limited, the amount of energy available for reproduction may be dependent on the foraging efficiency of an individual rather than on its size. The mean number of ripe ovarian eggs was only marginally higher than the mean number of abdominal eggs. This small difference may be due to the fact that not all ova are extruded as a number of the examined "spent" ovaries contained several resorbing large yolky eggs. Additionally, egg loss may occur during spawning due to the failure of some eggs to attach to pleopods. Similar fecundity studies in various crayfish species found abdominal egg counts to be lower than ovarian egg counts (Prins, 1968; Morrissy, 1975; Rhodes & Holdich, 1982; Hamr, 1983).

Since large females carry overall larger broods it appears that the size of female  may play an important role in determining the number of eggs which is actually attached to the pleopods, ie: larger females have larger abdomens with larger pleopods and more numerous oosetae and therefore more space for egg attachment.

Ovarian egg counts therefore present us with the potential fecundity of a species (given adequate energy stores and no egg loss) while juvenile counts give us the best estimate of the "real" fecundity of a species.

In summary, the reproductive cycles of *Astacopsis* and *Parastacoides* are generally characteristic of the life histories found in crayfishes living in high latitude, cold water environments (Momot, 1984). The species studied have a markedly prolonged breeding cycle, a long generation time (see Chapter 8), mature at a relatively large size and age and produce a generally small number of large yolky eggs (seemingly high in nutrient reserves). In *A. gouldi* higher fecundity may be offset by high mortality during the long time spent in immaturity, when crayfish are more active, have an increased moulting frequency and thus are more vulnerable to factors such as predation, environmental stress, competition for food and shelter.

CHAPTER 7 : REPRODUCTION / EMBRYONIC AND POSTEMBRYONIC DEVELOPMENT

7.1 INTRODUCTION

Copulation, spawning, egg and development of larvae have been well documented in many species of northern hemisphere crayfishes and marine lobsters (Andrews, 1907; Crocker & Barr, 1968; Mason, 1970A & B; Ingle & Thomas, 1974; Farmer, 1974; Pippitt, 1977; Atema & Cobb, 1980; Aiken & Waddy, 1980; 1986; Phillips & Sastry, 1980; Arrignon, 1981; Price & Payne, 1984; Holdich & Reeve, 1988; Köksal, 1988).

Egg attachment, embryology as well as the larval development have been studied in several Australian and South American parastacids (Clark, 1937; Hopkins, 1967A; Johnson, 1979; Rudolph & Zapata, 1986; Rudolph & Rios, 1987). Gurney (1935, 1960) examined several larval parastacids pointing out a major difference between Northern and Southern hemisphere crayfishes in the mode of attachment of the young to the female's pleopods. Mating, spawning and brooding in *Cherax destructor* have been well documented (Lewis, 1976; Johnson, 1979; Hosking, 1980; Lake & Sokol, 1986; Sokol, 1988; Mills, 1989). Sammy (1988) described the courtship, mating and brooding behavior of the tropical *C. quadricarinatus*. Shipway (1951) recorded the deposition of the spermatophore in *C. tenuimanus*.

In contrast, little is known about copulation, spawning and egg or larval development in the Tasmanian Parastacidae. Suter (1977) described in detail the development of the larvae in *Engaeus cisternarius* but did not observe spawning or copulation. Lake and Newcombe's (1975) ecological study of *P. t. tasmanicus* included some information on the larval development, but did not describe the developmental stages in detail.

This chapter examines copulation and spawning as well as embryonic and larval development of the Tasmanian crayfishes in the genera *Astacopsis* and *Parastacoides*. The reproductive biology and development of the two genera are compared to each other as well as to other members of the Parastacidae, Astacidae, Cambaridae and Nephropidae.

7.2 METHODS

Field observations of reproductive activity and behavior as well as egg and larval development were taken during regular sampling.

Prior to and during the mating season of each species, pairs of reproductively active males and females were set up in the laboratory to investigate courtship, copulation and spawning in each *A. gouldi*, *A. franklinii* and *P. t. tasmanicus*. Males were generally larger than females and were removed immediately following spawning. Several males which successfully copulated were paired with other females to determine whether multiple copulations can occur. A video camera/recorder connected to a timer was used for overnight observation of reproductive behavior in *Parastacoides*.

A number of ovigerous females of each of the three species were transferred to the laboratory where egg development, larval growth and duration of each stage were monitored (see Chapter 6). Females were held in environmental chambers where photoperiod, air and water temperatures were controlled. Development of eggs/larvae was checked daily and a small number of eggs or young were removed periodically for detailed description of developmental stages. The morphology of embryos and larvae was described and illustrated with the aid of a binocular dissecting microscope fitted with a camera lucida and high power light sources.

The duration of larval stages was monitored in the laboratory at 15 to 18°C (see Chapter 6).

7.3 RESULTS

7.3.1 Copulation and spawning

A. Astacopsis gouldi and *Astacopsis franklinii*

Only two reproducing females of *A. gouldi* were paired up with males, but both pairings resulted in successful copulations followed by egg extrusions. The two females measured 134.6 mm and 153 mm CPL and both mated with the same male which measured 128 mm CPL. The matings took place on April 1 and May 1, 1987. Little aggression was observed during the encounters but the smaller of the two

females had fresh puncture marks on both chelae following copulation. Adult females collected in the field often bear such marks on one or both chelae.

Of the thirteen laboratory mating pairs of *A. franklinii* Eastern form set up (males and reproducing females), only four mated and all but one of the mated females extruded eggs successfully. In all cases males were larger than females. The level of aggression was relatively low between all pairs. Two nonreproducing females were also paired with males to observe whether males could distinguish between reproducing and nonreproducing females. As both females were attacked by males and eventually killed and cannibalised no further pairings of this nature were initialized.

The entire mating sequence was not observed in either species but various aspects of mating behaviour were noted in the field and laboratory. Courtship was observed in both species and consisted of males stroking females with antennae and chelae. In one *A. gouldi* mating pair, the male was observed turning around in front of a potential mate, presenting his chelae and tail alternately and pushing her gently with the tips of his chelipeds. This courting was observed as early as one month prior to copulation but in this case the larger female was nonreceptive until a month after the two were paired. Mounting of females was not observed, but in the one copulating pair of *A. franklinii* Eastern form collected in the field, the male was on top the female who was turned on her back so that their ventral thoracic surfaces faced each other. It appears therefore that during copulation the female turns or is turned onto her back, the male mounts her and extrudes the spermatophoric mass through his genital papillae (Fig. 7.1) onto her ventral surface. A plug of clear to white matrix is extruded first and into it is then extruded additional clear matrix containing sperm tubes.

The spermatophores of *A. franklinii* and *A. gouldi* are identical in appearance, consisting of paired elongated gelatinous masses attached to the inner surfaces of the coxae of the fourth pereopods, directly below the female's gonopores (Fig. 7.2). Each spermatophore consists of clear matrix containing convoluted sperm tubes. The location of attachment appears to be specific as all freshly spawned females in the field and the laboratory had spermatophores attached to the coxae of the fourth walking leg. The spent spermatophores were normally lost within three days of mating.

The complete spawning behaviour was observed in only one *A. gouldi* female

Figure 7.1 Extruded spermatophore of A. franklinii.

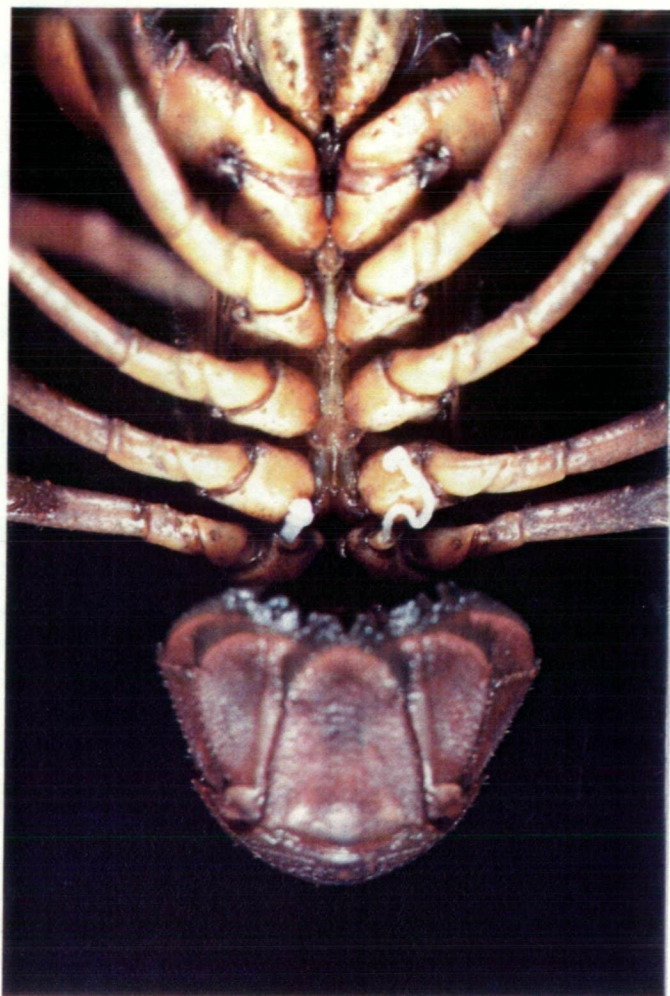
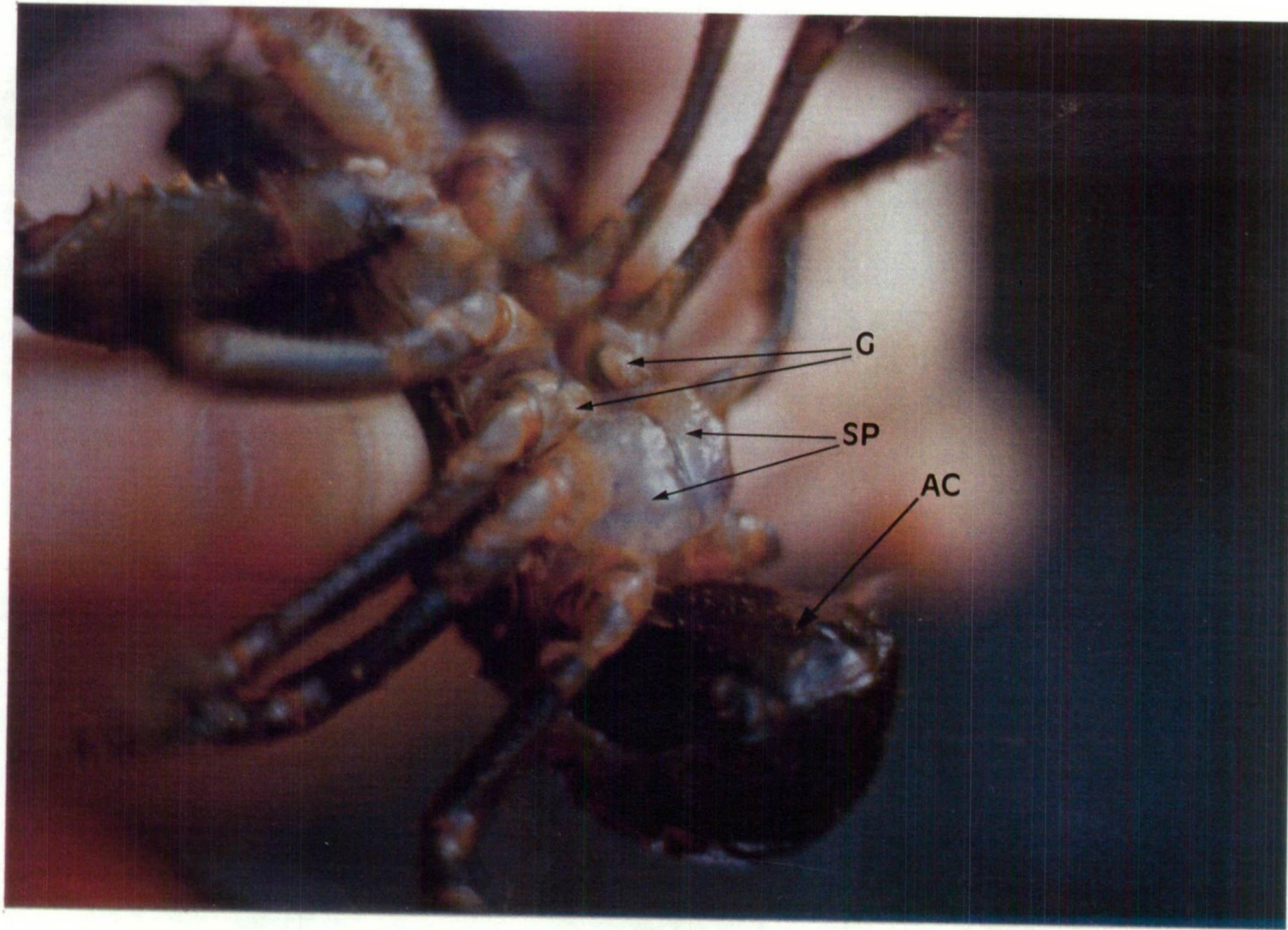


Figure 7.2 Spermatophore on coxae of female A. franklinii from Hobart Rivulet.

G = gonopore, SP = spermatophore, AC = abdominal cup or brood chamber.



but overall two *A. gouldi* and three *A. franklinii* spawned in the laboratory. In all cases copulation and spawning occurred overnight but in the single observed case spawning was not initiated until noon the next day. The following is the general sequence of events observed during spawning: the female turns onto her back, her abdomen is flexed so that the tail fan reaches just under her gonopores and eggs are extruded into the cup formed by the abdominal terga and tail fan. Once a female assumes the spawning position she supports herself with her chela and walking legs so that the anterior of her body is slightly raised to create a gradient sloping toward the abdominal "brood chamber". When all the eggs are extruded, the abdomen is cupped tightly forming an apparently watertight chamber in which ova and associated secretions are enclosed. This is accomplished by tight folding of the abdominal segments which are heavily fringed by setae. The tail fan is folded under and pushed up against the posterior of the coxae of the last pair of legs (Fig.7.2). The uropods are locked into position by the lateral, shield shaped epimeral plates which make up a part of the cephalothorax-abdomen hinge. After eggs are enclosed in this brood chamber the female begins a prolonged period of "turning" during which she rolls onto her side switching sides at regular intervals. This behavior, which was also observed in several freshly spawned *A. franklinii*, continued for several days following egg extrusion. It appears that the content of glair glands may be extruded into the chamber at this time and the rolling aids in the attachment of eggs to the pleopods. The abdomen remains tightly cupped for several weeks after extrusion and is extended only once the eggs are firmly attached to the pleopods.

The abdomen was forcibly extended in several females after spawning was complete to reveal still unattached soft ova floating in a clear liquid. Glair glands were less pronounced in these females indicating that their contents may have been extruded. It is important to note that the broods failed in all cases where the eggs were examined by forcible extension of abdomen. This indicates that breaking of the sealed brood chamber is detrimental to normal egg attachment and brood viability. In females where broods were not disturbed, eggs attached normally and remained viable throughout the period of incubation.

B. *Parastacoides tasmanicus*

The burrows of *P. t. tasmanicus* (SP) normally contain only one adult per burrow system. During the mating season however males and reproductive females pair off in burrows prior to copulation. In samples taken in March-April 1987, 30% of excavated burrows were empty. Pairing usually occurs as females prepare for the prereproductive moult: 80 % of paired females in February-March were busters or softshells (see Chapter 8). At the peak of mating activity (in March) 75 % of reproducing females and 56 % of large mature males caught were paired. Overall 23 mating pairs of *P. t. tasmanicus* (SP) were collected in the field from late February to early April. Copulating pairs were made up of generally large animals (Figure 7.3) and in 17 out of the 23 pairs (74 %) males were of the same size or larger than females. The largest size difference occurred in a pair found in late February where the male measured 24.3 mm CPL and the female 30 mm CPL. In three cases burrows contained three animals, in each case one female and two males. In two of these triplets one of the males was considerably smaller (female CPL 30 mm, males CPLs 31 and 24 mm; female CPL 32.2 mm, males CPLs 31.6 and 26 mm) while in the remaining triplet all three crayfish were of similar size (female CPL 31 mm, males CPLs 31.5 and 30.7mm).

Of the 23 laboratory mating pairs (males and reproducing females) of *P. t. tasmanicus* (SP), 15 copulated, and of these, 9 extruded eggs successfully. In all cases males were the same size or larger than females. One of the males successfully copulated with two females within a period of two weeks. There was no aggression observed in any of the pairs. Several nonreproducing females were also paired with males to observe whether males could distinguish between reproducing and nonreproducing females. No copulation occurred in these pairs but there was also no significant aggression observed although females generally avoided males.

All copulations occurred overnight, usually within shelters, and therefore only one encounter was successfully recorded on video tape. Courtship behaviour was observed and recorded in numerous pairs and, as in *Astacopsis*, it consisted of males stroking females with antennae and chelae. In the one recorded mating sequence the male mounted the female which had turned onto her back. The copulation lasted approximately ten minutes and proceeded without any apparent struggle or grasping with chelae on the part of the male. When the spermatophore was deposited the male dismounted and the female turned over. The female did not spawn following this

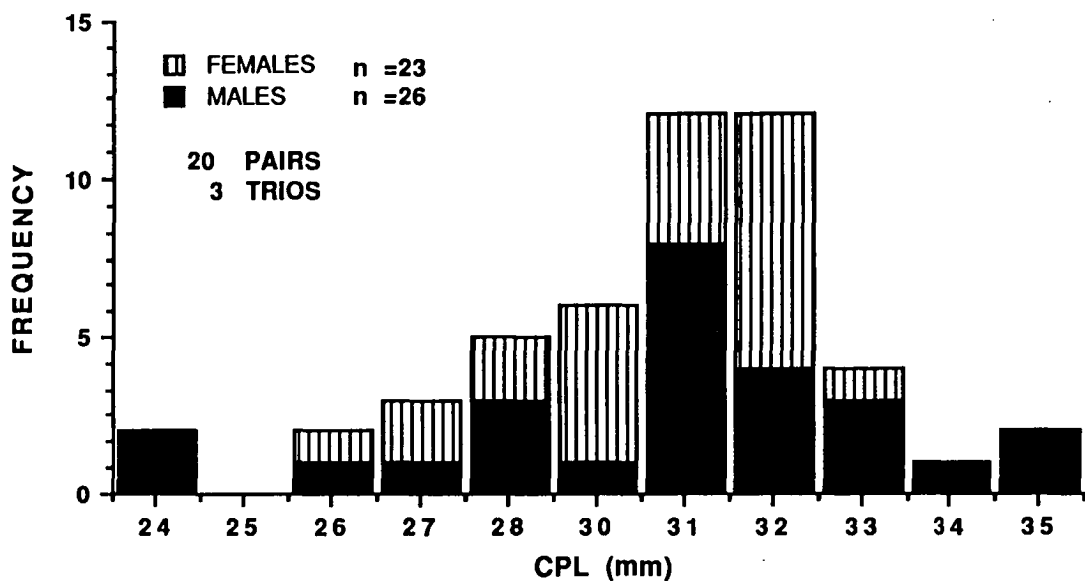


Figure 7.3 Carapace lengths of males and females in mating pairs of *Parastacoides t. tasmanicus* (SP) from Harlequin Hill, South West Tasmania. (February-April, 1986 & 1987).

mating.

The spermatophore of *P. t. tasmanicus* (SP) is roughly heart-shaped, relatively small, gelatinous and well-attached. It is always attached to the sternal processes between the fourth pereopods, directly below the female's gonopores (Fig. 7.4). The spermatophore consists of a clear matrix containing convoluted sperm tubes. The spent spermatophores were smaller, soiled brown and were usually lost completely only several weeks after mating.

Spawning was not witnessed in any of the pairs but it always occurred shortly after mating, as mating and spawning always occurred during the same night. As in *Astacopsis*, the abdomen and tail fan were folded into a brood chamber to protect the freshly spawned eggs. Turning behavior, as described for *Astacopsis*, was observed in one freshly spawned female the morning after a night spawning. The abdomen was forcibly extended in another freshly spawned female to reveal still-unattached soft ova. The glair glands of this female were still pronounced indicating that their contents were not yet fully extruded. Glair may therefore be extruded some time after spawning. Several field-collected females with fresh broods and old spermatophores also had the remains of a sticky mucus like material (presumably glair) present in their brood chambers. As in *Astacopsis* the broods failed in most cases where eggs were examined by forcible extension of the abdomen. In females where broods were not disturbed, eggs attached normally and remained viable throughout the period of incubation.

7.3.2 Fertilization and egg attachment

Eggs were probably fertilized as they passed over the spermatophore on their way to the abdominal brood chamber. Examination of fresh spermatophores on unspawned females revealed that sperm tubes filled with sperm were completely enclosed in the surrounding clear matrix. In contrast, spent spermatophores had their outer surface partly dissolved, exposing the ends of empty sperm tubes. It appears, therefore, that during spawning some of the spermatophore is dissolved away and sperm is thus released from the convoluted sperm tubes. This probably happens as the eggs and associated fluids pass over the spermatophore.

As in other decapods, eggs are attached to, and carried on, the four pairs of

abdominal pleopods (Figs. 7.4 & 7.5). The actual egg attachment to pleopods could not be observed, but probably occurs during the "turning" phase of spawning, at which time the content of the glair glands is also released into the brood chamber. Remains of this glair were seen in several freshly spawned females. Eggs are attached to the long filamentous oosetae found on pleopods (Figs. 7.7B & 7.8A). In *Astacopsis* the oosetae are mainly present on the basipodite and endopodite and to a lesser extent on the exopodite, while in *Parastacoides* they only occur on the basipodite and endopodite. The oosetae are twisted and bound together by a sticky white substance which is presumed to be the glair gland secretion (Fig. 7.7C). The twisted setae bound by secretion form egg stalks which attach via setal tips to the clear egg case surrounding each ovum (Figs. 7.7B-C & 7.8A).

7.3.3 Embryonic development

A. *Astacopsis*:

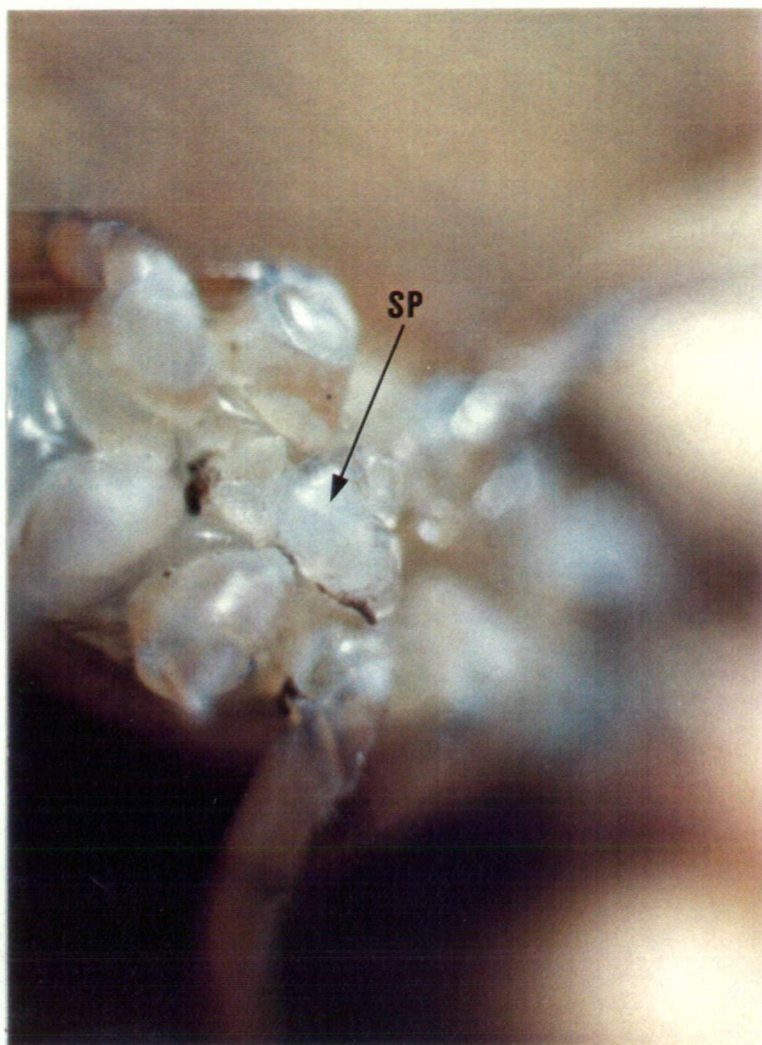
The sequence of embryonic development in *A. gouldi* is shown in Figure 7.6. When first extruded the eggs are elongated, purple brown in colour with uniform yolk distribution and covered with a very thin fragile membrane (Fig. 7.6A). Once the eggs are attached to the pleopods via the egg stalk, they become less elongated and are covered by a thicker membrane. When the embryo begins to develop, the yolk immediately adjacent to it changes colour to a very dark brown (Fig. 7.6B). As the embryo develops further the proportion of dark yolk enlarges until eventually the whole egg is dark purple-brown in colour (Fig. 7.6C-D). During its development the embryo undergoes changes in morphology from an embryonized nauplius through to a fully formed stage 1 juvenile. The embryonized nauplius takes up a very small portion of the total egg volume and has rudiments of thoracic appendages. As the embryo grows, the carapace, abdomen and associated appendages develop until the fully formed embryo stage is reached. These development stages correspond to embryonized protozoa and mysis (zoa) stages described in previous studies (Huxley, 1880; Johnson, 1979). Just before hatching, most body parts and some organs can be distinguished, the eyes are prominent and pigmented, the heartbeat can be discerned and the embryo now occupies about half of the total egg volume (Fig. 7.6E).

Figure 7.4 Spermatophore of *P. t. tasmanicus* (SP).

A. Freshly extruded, heart-shaped spermatophore on female just prior to spawning.

B. Spent, eroded, and soiled spermatophore on spawned female.
Note freshly extruded eggs attached to abdominal pleopods.

A



B

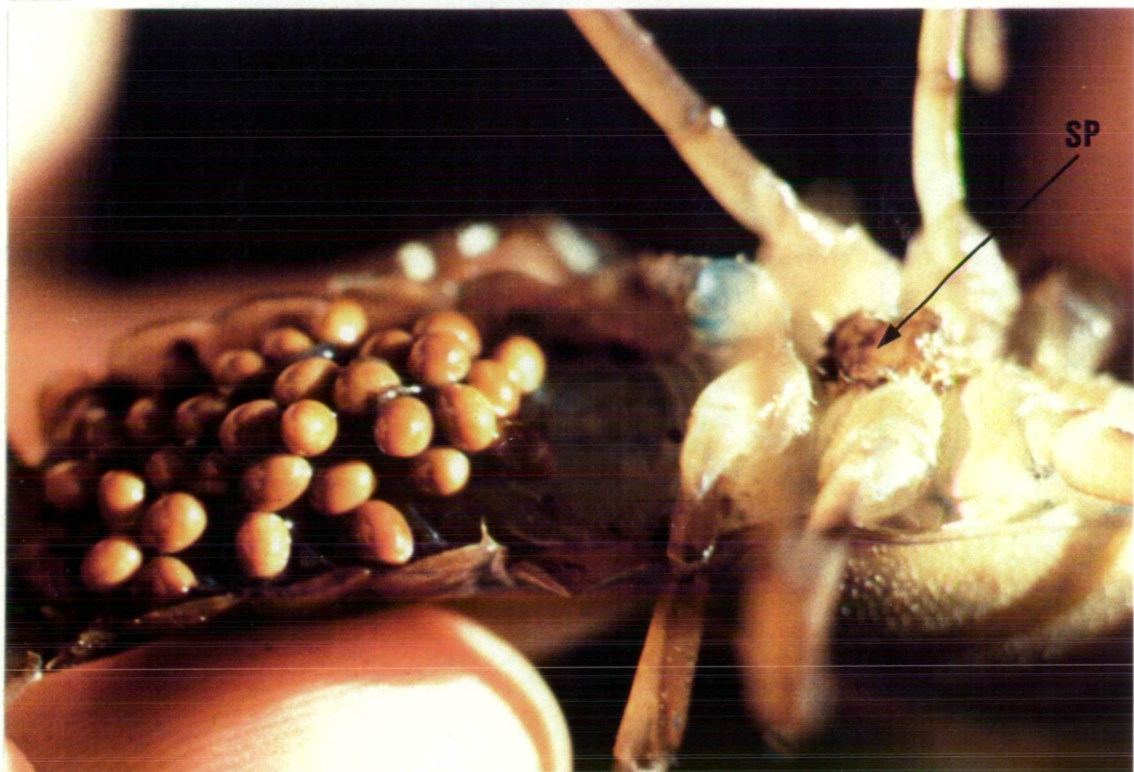


Figure 7.5 Ventral view of ovigerous A. gouldi female (CPL 121 mm), showing well attached brood within the uncurled brood chamber. Note wide abdominal segments with heavy setal fringes on edges.



Figure 7.6 Embryonic development in *Astacopsis gouldi*:

A. Freshly extruded (few hours old) unattached egg. **B.** Egg with early embryonized nauplius embryo. **C.** Egg with early embryonized protozoa embryo. **D.** Egg with late embryonized protozoa embryo. **b** Egg with fully formed embryo just prior to hatching (eyes pigmented).

Abbreviations for Figures 7.6 - 7.8:

Em: embryo

DY: dark coloured yolk

LY: light coloured yolk

OS: ooseta

E: egg

ES: egg stalk

EC: egg capsule

J: juvenile

L: walking leg

An: antenna

Ant: antennule

C: cheliped

Ey: eye

Hp: hepatopancreas

A: abdomen

PL: pleopod

G: glair

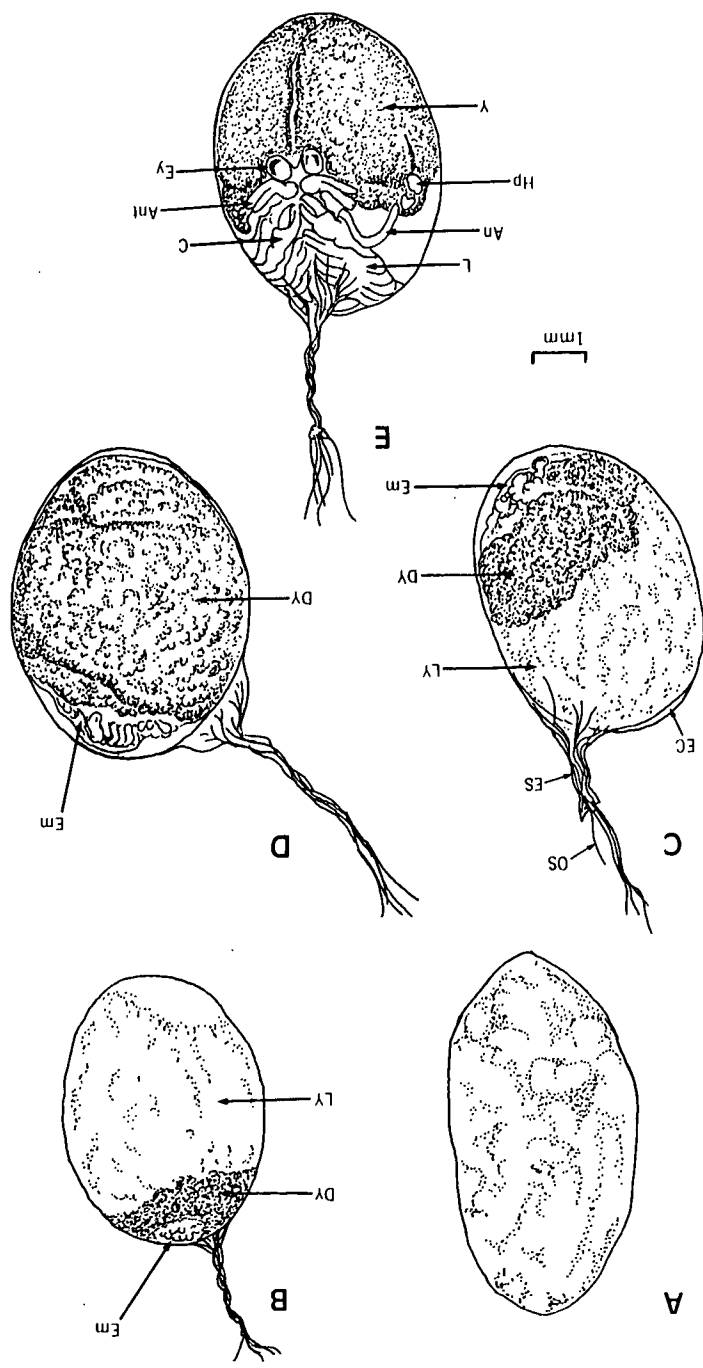


Figure 7.7 Embryonic development, egg attachment and hatching in *Astacopsis franklinii*.

A. Pleopod of berried female, E1: egg with protozoa embryo, E2: egg with early mysis embryo.

B. Egg with early embryonized nauplius embryo.

C. Egg with fully formed embryo just prior to hatching (eyes pigmented).

D. Hatching young.

E. Twin embryo 1: top view, 2: lateral view.

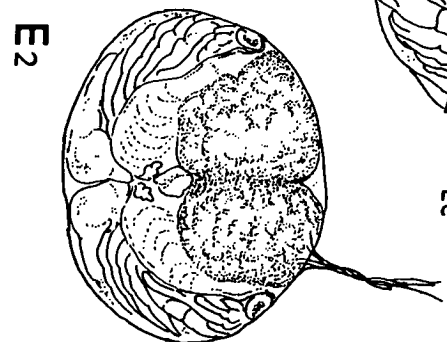
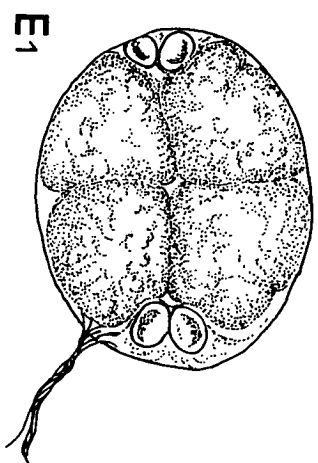
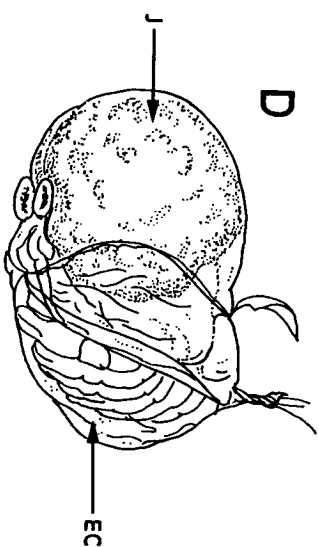
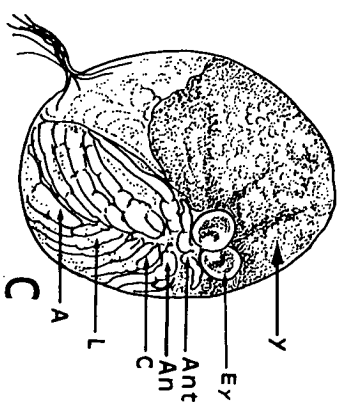
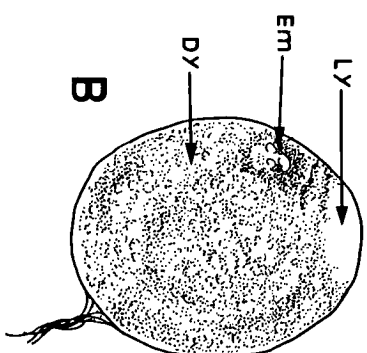
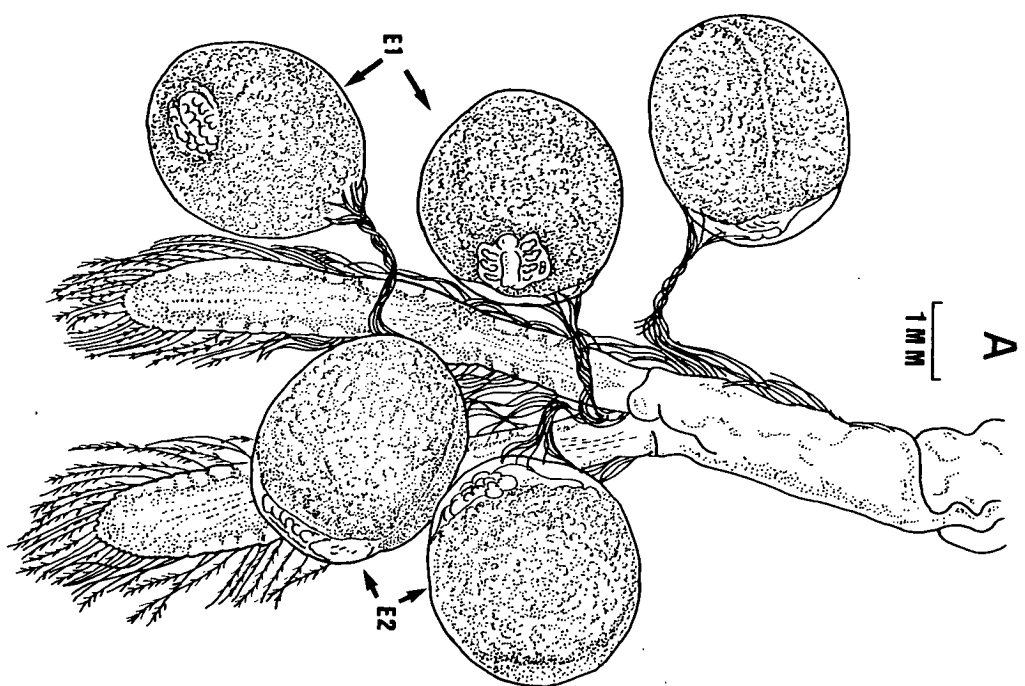


Figure 7.8 Embryonic development, egg attachment and hatching in *Parastacoides t. tasmanicus*.

A. Embryonic development:

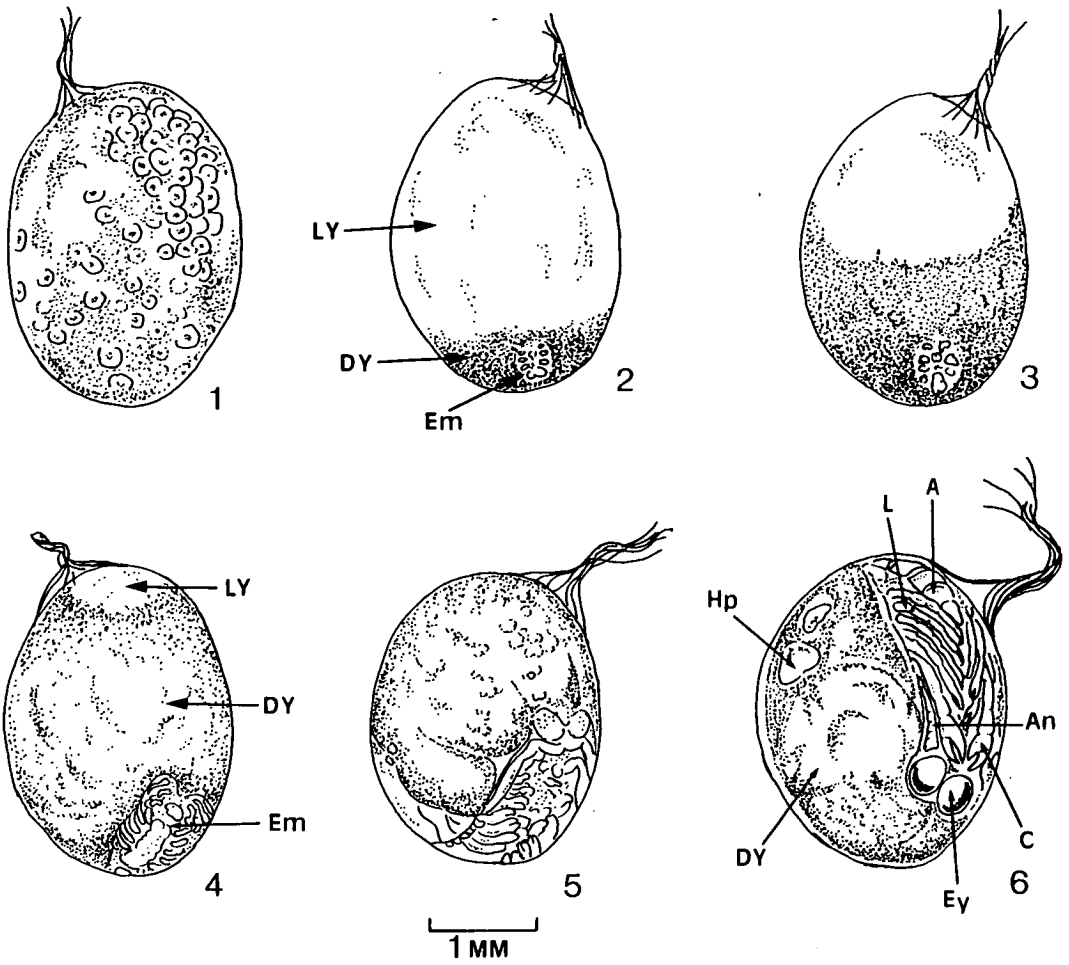
1. Egg in early development showing cleaving nuclei.
2. Egg with early embryonized nauplius embryo.
3. Egg with embryonized nauplius embryo, yolk darkening.
4. Egg with embryonized protozoa embryo .
5. Egg with embryonized mysis (zoea) embryo.
6. Egg with fully formed embryo just prior to hatching (eyes pigmented).

B. Pleopod of berried female showing four late eggs and one empty egg capsule.

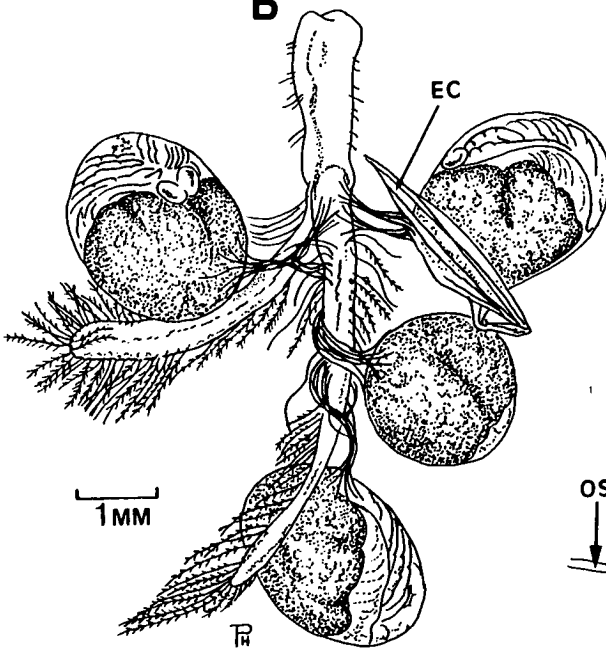
C. Detail showing mode of egg attachment.

D. Detail of oosetae showing glair globules.

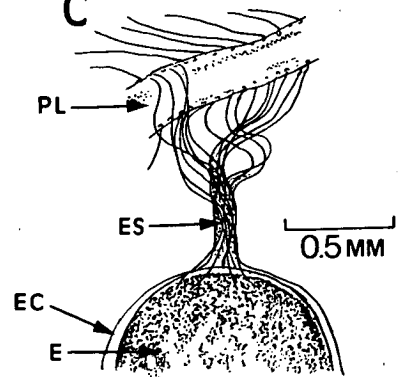
A



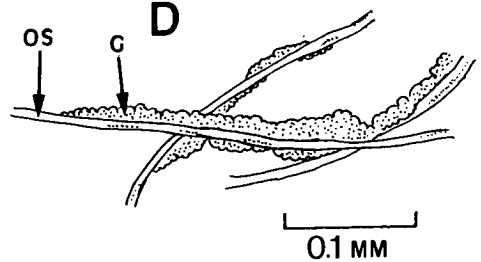
B



C



D



The stages of egg and embryo development in *A. franklinii* (Eastern form) correspond to those described for *A. gouldi* (Fig. 7.7A-C). Freshly extruded eggs are light brown-yellow and turn dark orange-brown during development. The embryo undergoes the nauplius-protozoa-mysis development stages to reach a fully formed stage just before hatching.

An interesting facet of *Astacopsis* embryonic development was the presence of twins formed from the same egg (Fig 7.7E). Eggs containing advanced twin embryos were found on two *A. franklinii* females from Hobart Rivulet with one of these females carrying two such eggs (out of a brood of 94). One twin egg was also found on a *A. gouldi* female from the Inglis River. It could not be determined whether these eggs could hatch successfully but close examination revealed that both embryos had a fully formed complement of body parts and organs.

B. *Parastacoides*:

The sequence of embryonic development in *P. t. tasmanicus* was similar to that described for *Astacopsis* and is summarized in Figure 7.8. Freshly extruded eggs were light yellow-brown and turned darker orange-brown during development. As in *Astacopsis*, the embryo undergoes the nauplius-protozoa-mysis development stages to reach a fully formed stage 1 juvenile just before hatching.

7.3.4 Postembryonic development

A. *Astacopsis gouldi*

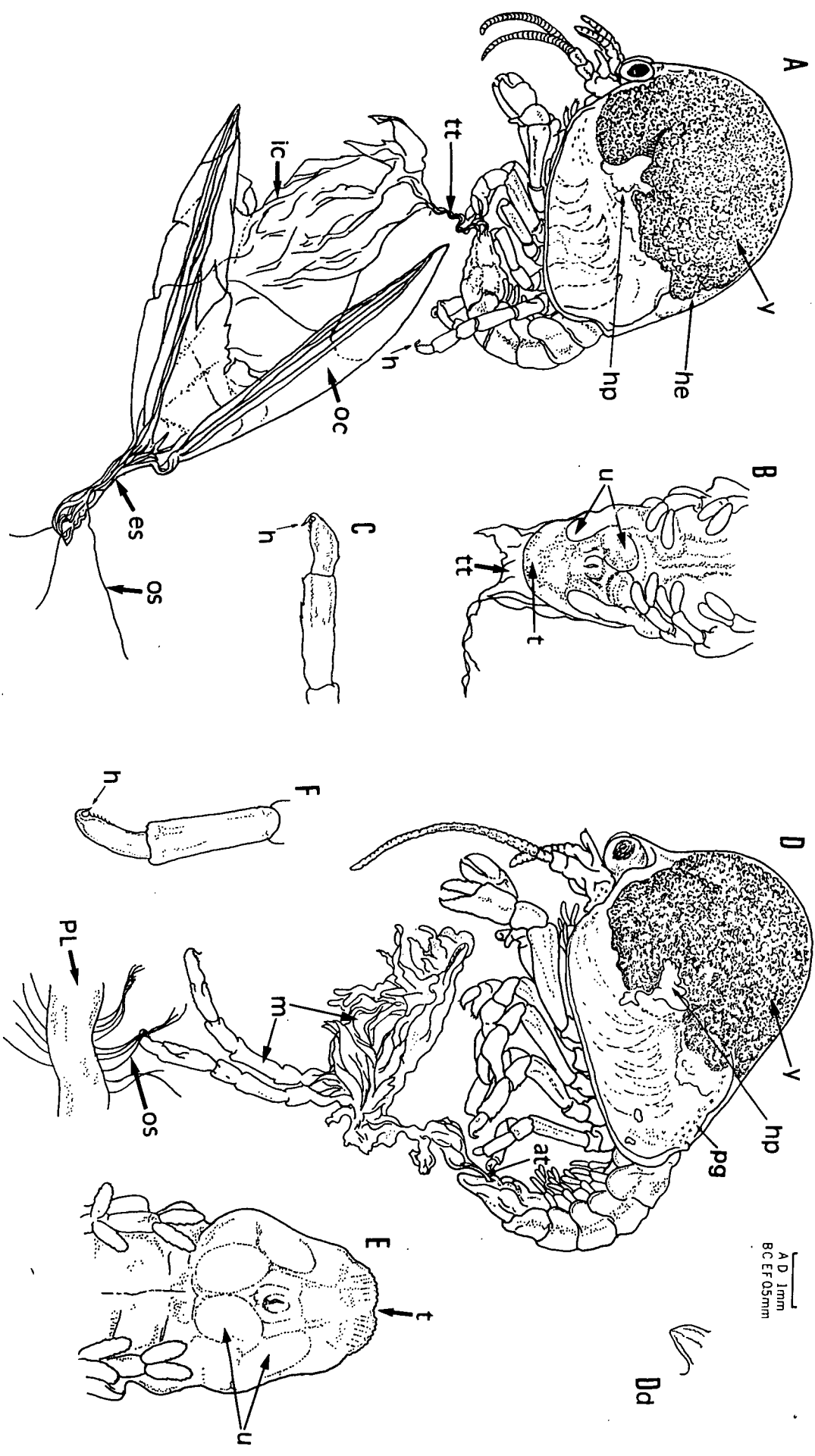
Stage 1: Hatching occurs by splitting of the egg capsule along the dorsal side of the embryo so that the young emerge backwards with the appendages and abdomen becoming free last (Fig 7.7D). The split egg case usually remains attached to the oosetae for some time, in some cases until the young become independent. The freshly emerged juvenile remains attached to the inner lining of the egg capsule by a thin thread connected to the tip of its telson (Fig. 7.9A&B). This "telson thread", formed by the twisting of the inner capsule lining, acts as a safety line during hatching, thus preventing the young from dropping away from the pleopod. There appear to be no special structures on the telson edge for the attachment of the thread.

Figure 7.9 Stage 1 young of *Astacopsis gouldi* from the Inglis River:

- A.** Early stage 1 young and egg capsule. Note telson thread connection to egg capsule.
- B.** Telson of early stage 1.
- C.** Tip of fifth pereopod of early stage 1.
- D.** Late stage 1 young and moult . Note anal thread connection to moult.
- E.** Telson of late stage 1.
- F.** Tip of fifth pereopod of late stage 1.

Abbreviations for Figures 7.9 - 7.17:

at: anal thread
es: egg stalk
g: gastrolith
h: recurved hook
ho: hooklets
he: heart
hp: hepatopancreas
ic: inner egg capsule
m: moult
oc: outer egg capsule
os: oosetae
p: papilla on telson
pg: pigment
s: setae
st: stomach
t: telson
tt: telson thread
u: uropods
y: yolk
PL: pleopod of mother



Soon after hatching, the young attaches itself to the pleopodal setae by specialized hooks on the tips of its fourth and fifth pereopods (Fig. 7.9A&C and 7.12B). The oosetae are hooked under a specialized recurved spine and prevented from slipping out by small hooklets in a clip-like fashion (Fig. 7.12G). The telson thread is usually broken within a few days of hatching. The stage 1 young is embryonic in its general appearance, having a rounded carapace filled with yolk, a short downcurved rostrum, stalkless eyes, short antennae and antennules, and no visible setae or pigmentation (Fig. 7.9A). The tailfan is undifferentiated, consisting only of the telson which has no setal buds on its outer edge (Fig. 7.9B). The forming buds of the uropodal rami can be seen within the tailfan. The development of the uropods is unusual in that a prominent papilla just posterior to the anus contains the folded inner uropodal rami. The outer rami can be seen forming laterally within the tailfan. (Fig.7.9B). Pleopods are small and without setal buds.

The young are small and not very active at this stage with a mean carapace length of 4.96 mm (s.d. = 0.36 , n = 10, range = 4.6-5.4). Two to four days after hatching, the stage 1 young moults into a more advanced state with morphological characters intermediate between stage 1 and 2. The advanced or "late" phase differs from the "early" phase by being larger and having partly stalked eyes, a more prominent rostrum and small amount of pigmentation around the areola (Fig. 7.9D). Major differences can also be seen in the telson which now has setal buds on its tip, and the uropodal buds are easily detected within the telson and its papilla (Fig. 7.9E). Pleopods develop setal buds and the rostral ridge characteristic of the species can also be first seen at this time. The mean carapace length of late stage 1 young was 5.7 mm (s.d. = 0.19 , n = 16 , range = 5.4-5.9).

During the moult from early to late stage 1 the newly moulted young remained attached to the old cuticle by a thin thread connecting the anus of the juvenile to its moult (Fig. 7.9D). Upon closer examination it was found that this anal thread is in fact the old cuticular lining of the intestine of the early stage 1 larva still attached to the intestine of the late stage 1 larva. The anal thread therefore acts as a safety line during the moult as the young are tethered to the mother by their moult which is still attached to the mother's pleopods via the hooks on its pereopods (Fig. 7.9D).

Stage 2: After a further 7 to 9 days spent in late stage 1 the young moult again to reach stage 2. During and just after the moult the young are again attached to their moults by an anal thread. Soon afterwards the young attach to the pleopodal setae by

the specialized hooks on the tips of its fourth and fifth pereopods (Fig. 7.10A&C). Stage 2 young are larger and more active than stage 1 young. The mean carapace length of stage 2 young was 6.3 mm (s.d. = 0.39 , n = 16 , range = 5.9-6.8). The carapace is more elongated and contains less yolk, the eyes are stalked, the body and appendages are weakly pigmented and setae can be seen on pereopods and maxillipeds. The tail fan is now differentiated consisting of a large telson and somewhat smaller uropods which bear setal buds on their outer edges (Fig. 7.10B).

Stage 3: After another 7 to 10 days the young moult again to reach stage 3. During and just after the molt the young are again attached to their mothers by an anal thread. Following the breaking of the anal thread the young hang on to their mothers by gripping pleopodal setae and each other with their chelae and walking legs. The hooks on the fourth and fifth pereopods are now less curved and cannot be effectively used to lock onto the setae (Fig. 7.11C). Stage 3 morphology is generally adult-like. Antennae are long, the uropods are completely developed, of the same length as the telson and their edges are heavily setose. The body and all appendages are also covered with numerous small setae. Pigmentation is present on the carapace, abdomen and all appendages. Initially the pigment is mainly orange brown, but later a heavy blue pigment is deposited on the body and to a lesser extent on the appendages. No sign of gonopore development is evident at this stage. The mean carapace length of stage 3 young was 7.3 mm (s.d. = 0.18 , n = 31, range = 7.2-7.5). The young are active, crawling about, and in advanced stage 3 they can be seen frequently leaving the female for short excursions. The period spent in stage 3 is about 35 days and young first begin venturing from their mothers at about day 28. Yolk is still present during stage 3, but its quantity is small, and it disappears completely by the time young moult to stage 4 and leave their mothers permanently.

B. *Astacopsis franklinii*

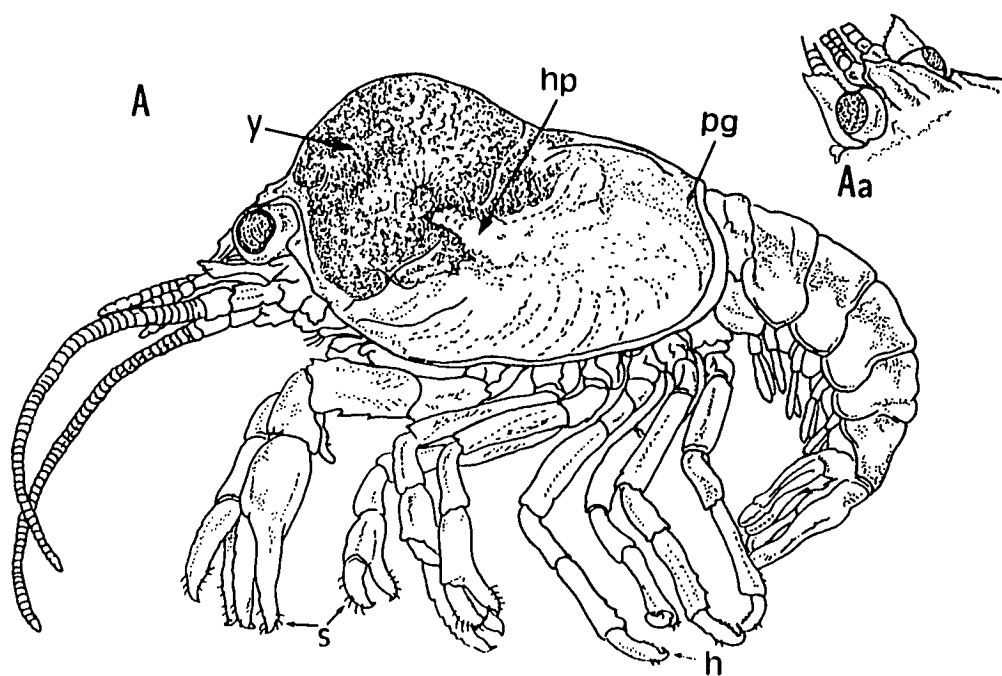
The hatching process and postembryonic development in *A. franklinii* is identical to that described for *A. gouldi* (Figs. 7.12-7.14). As in *A. gouldi*, stage one is divided into early and late by a moult in which the embryonic cuticle is shed (Fig. 7.12). The young of *A. franklinii* can be distinguished from those of *A. gouldi* by their smaller overall size and lack of rostral carina. The pigmentation of stage 3 juveniles is also more orange than in *A. gouldi*. The mean carapace length was 3.85 mm (s.d. = 0.1 , n = 15, range = 3.7-4.0) in early stage 1, 4.4 mm (s.d. =

Figure 7.10 Stage 2 young of *Astacopsis gouldi* from the Inglis River:

A. Stage 2 young, lateral view.

B. Tail fan of stage 2 young. Note differentiated tailfan with short uropods.

C. Tip of fifth pereopod of stage 2 young.



A 1mm
B C 0.5mm

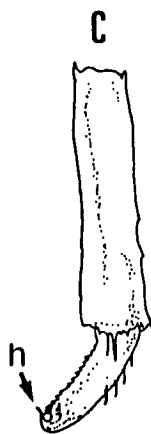
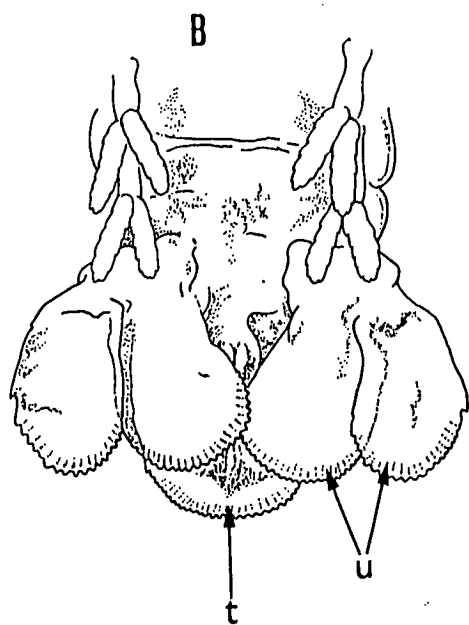


Figure 7.11 Stage 3 young of *Astacopsis gouldi* from the Inglis River:

A. Stage 3 young, lateral view.

Aa. Detail of rostral region .

B. Tail fan of stage 3 young. Note fully developed uropods with long setae.

C. Tip of fifth pereopod of stage 3 young. Note straightening of terminal spine.

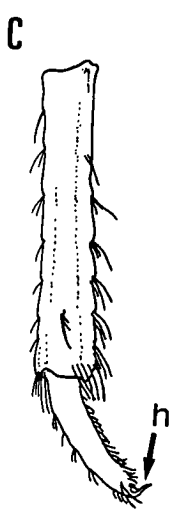
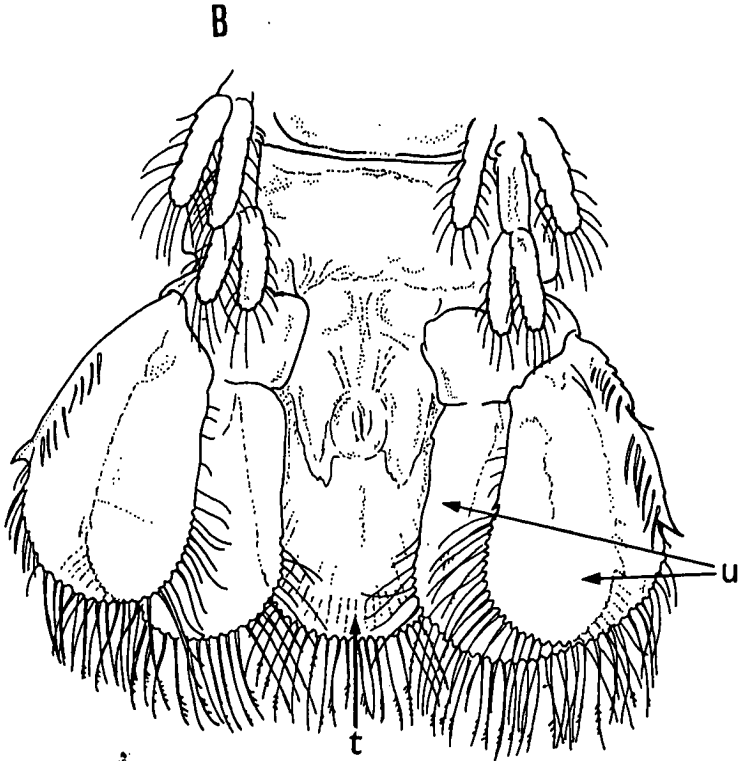
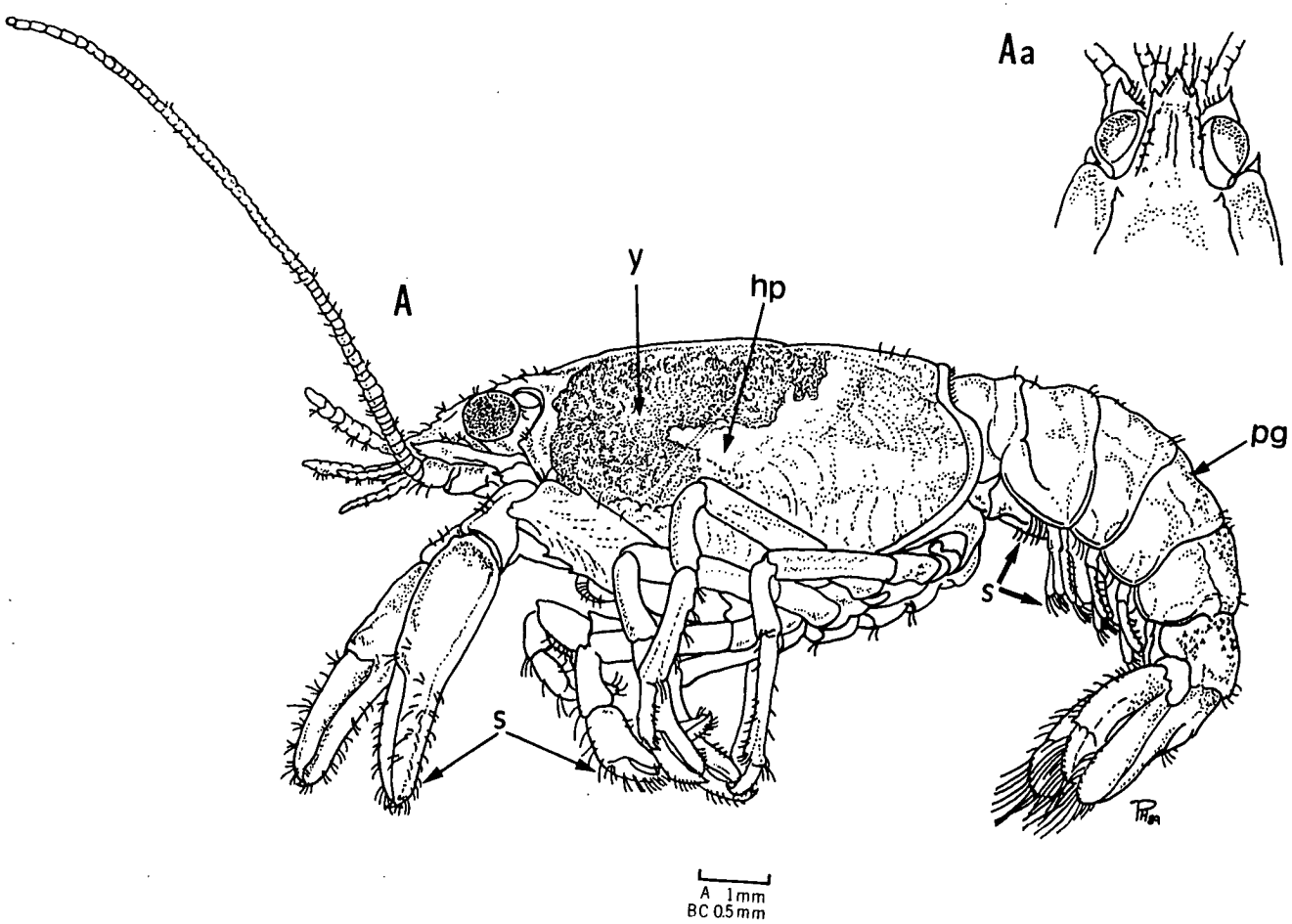


Figure 7.12 Stage 1 young of *Astacopsis franklinii* from Hobart Rivulet:

- A.** Early stage 1 young, lateral view.
- B.** Late stage 1 young attached to oosetae.
- C.** Tip of fifth pereopod of early stage 1 young.
- D.** Telson of early stage 1 young.
- E.** Tip of fifth pereopod of late stage 1 young.
- F.** Telson of late stage 1 young.
- G.** Detail of pereopod showing mode of attachment to oosetae

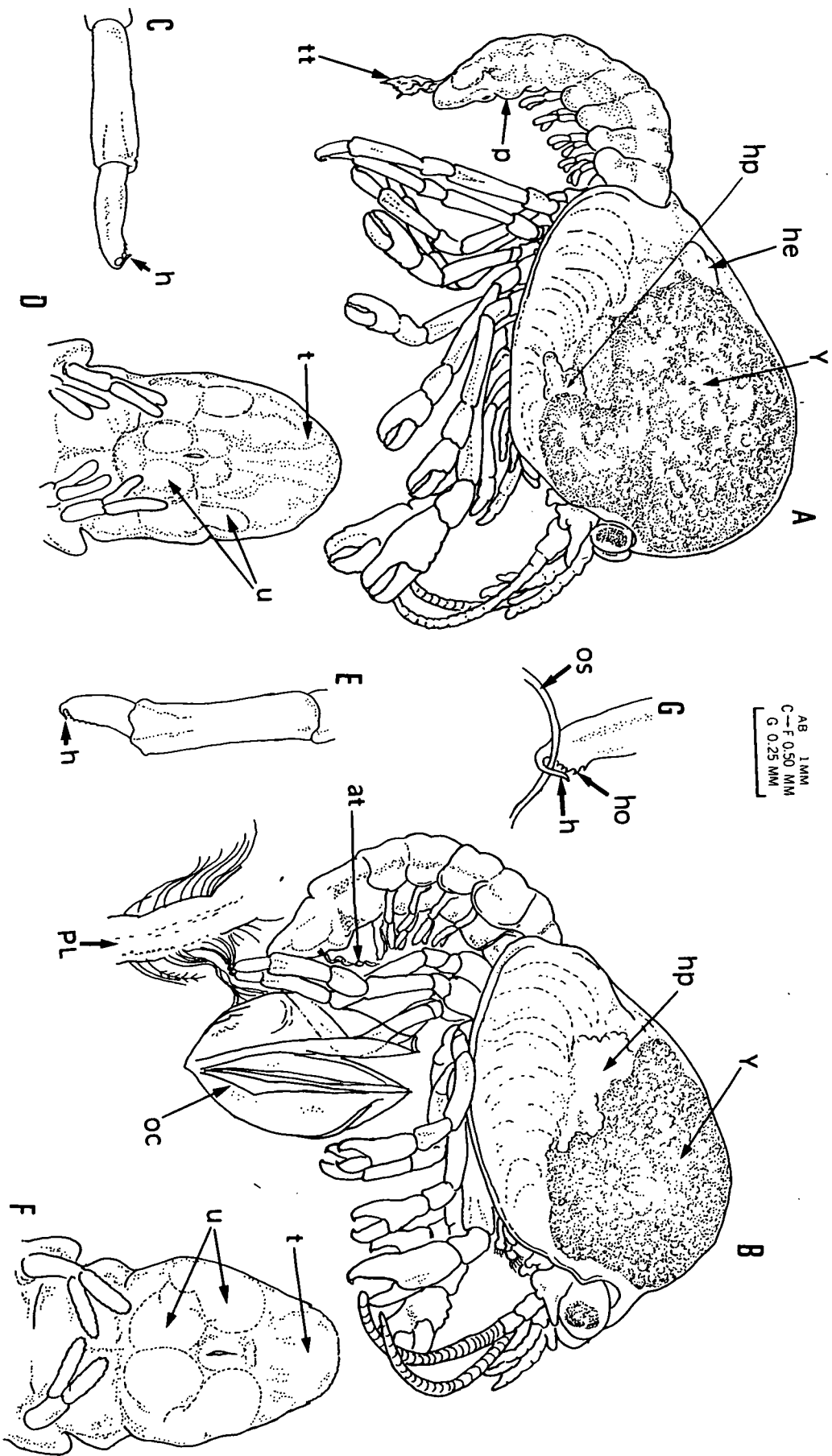
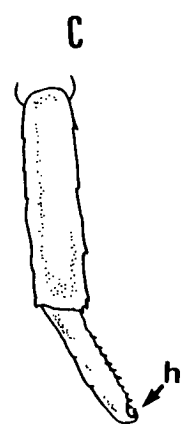
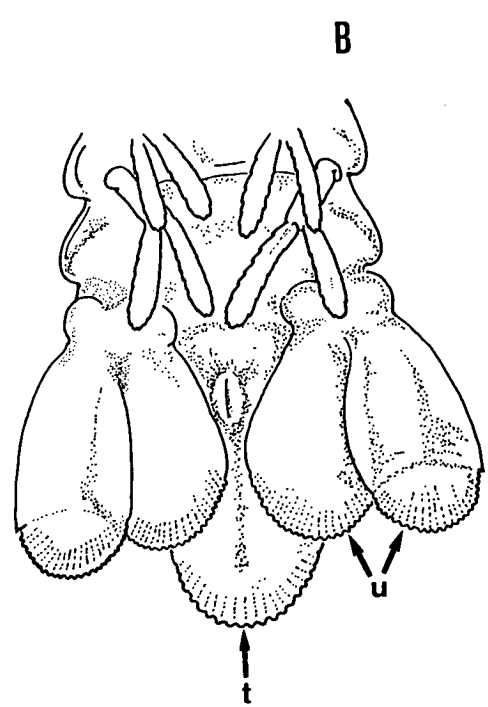
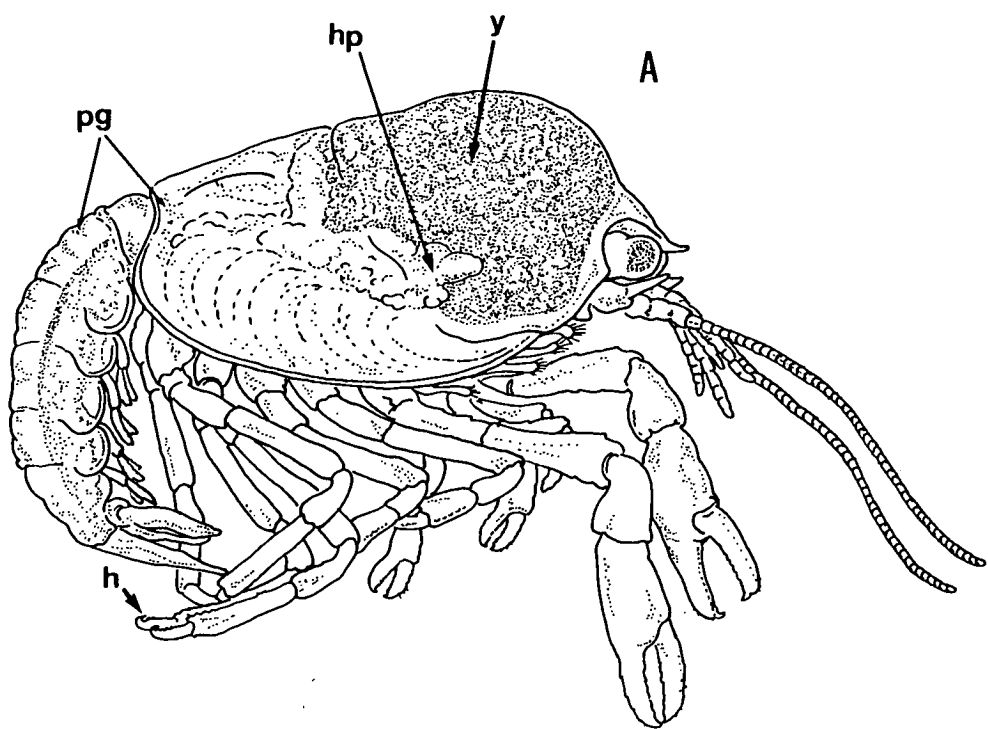


Figure 7.13 Stage 2 young of *Astacopsis franklinii* from Hobart Rivulet:

A. Stage 2 young, lateral view.

B. Tail fan of stage 2 young.

C. Tip of fifth pereopod of stage 2 young. Note differentiated tailfan with short uropods.



A 1MM
BC 0.5MM

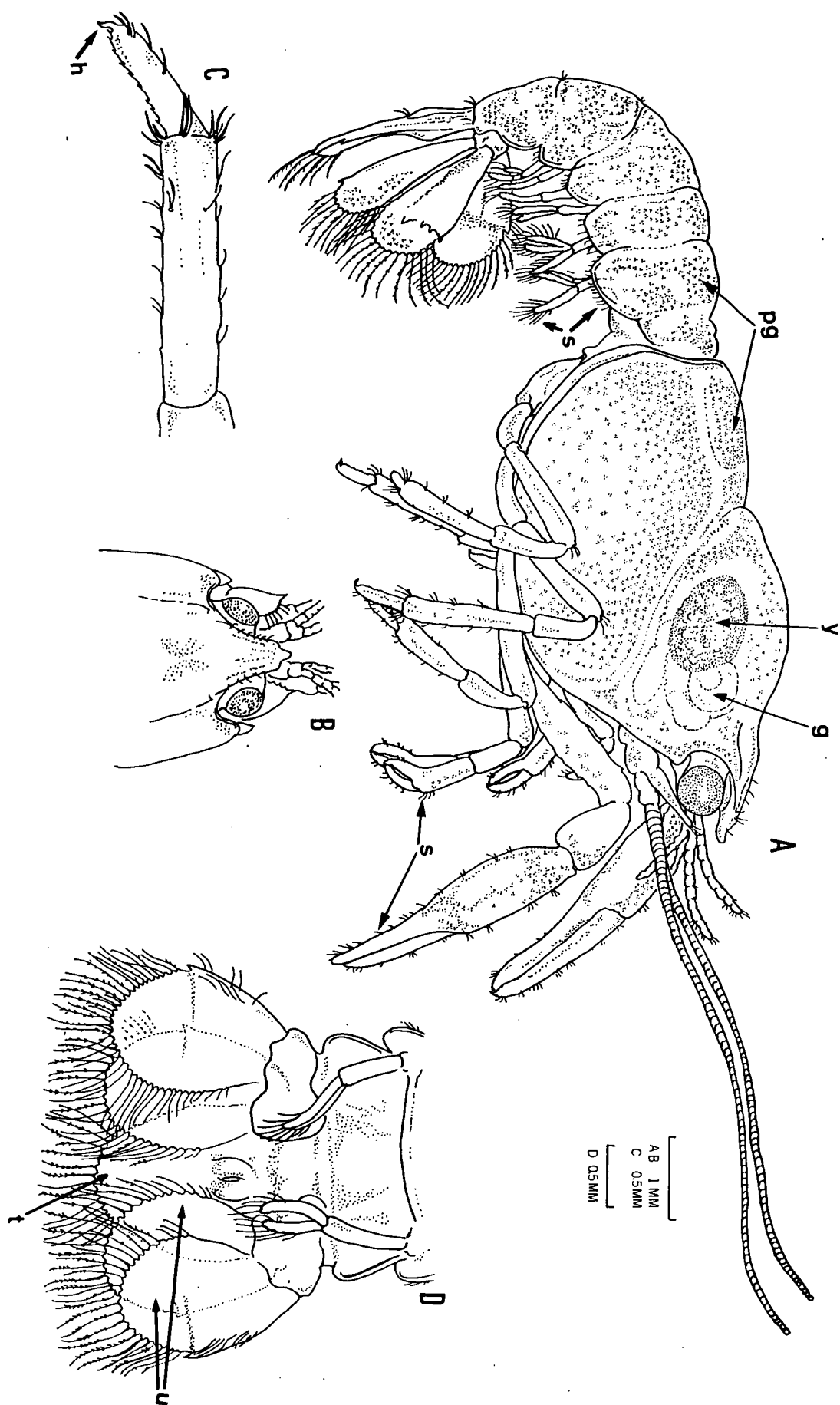
Figure 7.14 Stage 3 young of *Astacopsis franklinii* from Hobart Rivulet:

A. Advanced stage three young. Note small yolk and large gastroliths.

B. Detail of rostral region.

C. Tip of fifth pereopod of stage 3 young. Note straightening of terminal spine.

D. Tail fan of stage 3 young. Note fully formed setose uropods.



0.18, n = 15, range = 4.1-4.7) in late stage 1, 5.0 mm (s.d. = 0.32, n = 19, range = 4.5-5.25) in stage 2 and 5.39 mm (s.d. = 0.32, n = 56, range = 4.8-5.9) in stage 3 young. The time spent in each stage is comparable to *A. gouldi*.

C. Parastacoides t. tasmanicus

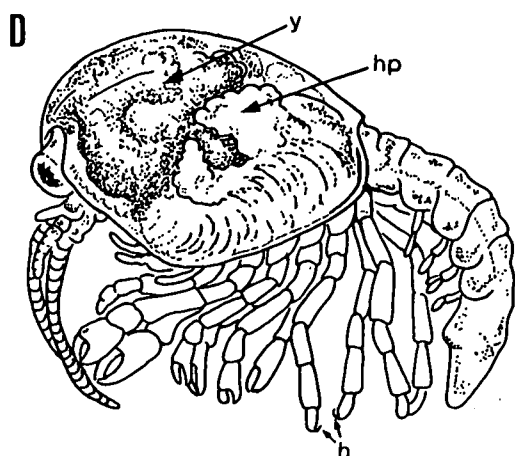
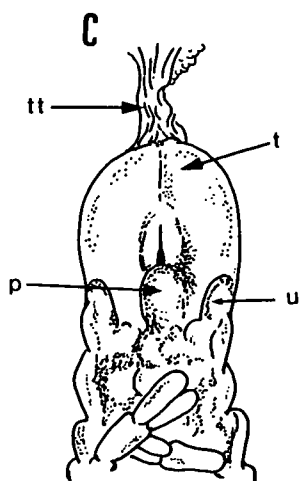
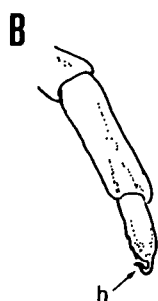
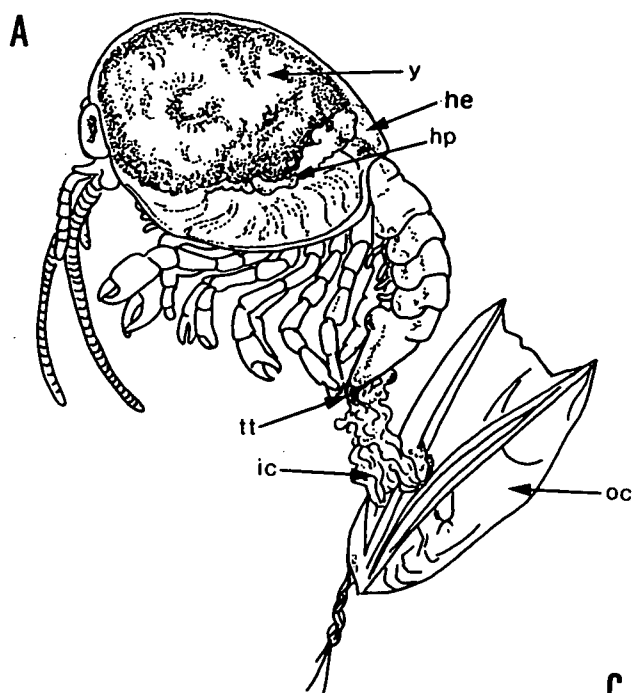
Stage 1: The hatching process in *Parastacoides* is similar to that described for *Astacopsis*. The egg capsule, which splits dorsally, has a thicker, lightly brown coloured outer layer and thin transparent inner lining. The inner lining remains attached to the tip of the telson of the juvenile and the portion closest to the telson forms the telson thread. There appear to be no special structures on the telson edge for the attachment of the thread. This connection is severed within 1-2 days of hatching and from then on the young hang on via the hooks on the tips of their fourth and fifth pereopods (Fig. 7.15B).

The stage 1 young has a rounded carapace filled with yolk, a short down-curved rostrum, stalkless eyes, short antennae and antennules and no visible setae or pigmentation (Fig. 7.15A). The tailfan is undifferentiated, consisting only of the telson which has no setal buds on its outer edge (Fig. 7.15C). The forming buds of the outer uropodal rami can be seen within the telson, which also has prominent papilla just posterior to the anus. This papilla contains the folded inner uropodal rami. Pleopods are small and without setal buds. The young are small and not very active, with a mean carapace length of 2.94 mm (s.d. = 0.08, n = 50, range = 2.8 - 3.1). The juvenile undergoes some changes before moulting to stage 2 but no intermediate moult was detected between stage 1 and 2. The advanced stage 1 young have a less rounded carapace, less yolk, larger hepatopancreas, eyes with short stalks and some pigmentation on edges of carapace and abdominal segments (Fig. 7.15D).

Stage 2: After 13 to 20 days spent in stage 1 the young moult into stage 2. During and just after the moult the young are attached to their moults by an anal thread. This thread is of the same origin as in *Astacopsis*. Soon afterwards, the young reattach to the pleopodal setae by specialized hooks on the tips of their fourth and fifth pereopods (Fig. 7.16C&F). Stage 2 young are larger and more active than stage 1 young. The mean carapace length of stage 2 young was 3.64 mm (s.d. = 0.09, n = 50, range = 3.5-3.8). The carapace is more elongated and contains less yolk, the eyes are stalked, the body and appendages are weakly pigmented and setae can be seen on pereopods and maxillipeds. The tail fan is still undifferentiated,

Figure 7.15 Stage 1 young of *Parastacoides t. tasmanicus* from Harlequin Hill, South-West Tasmania:

- A.** Stage 1 young, immediately following hatching, lateral view.
- B.** Tip of fifth pereopod of early stage 1 young.
- C.** Telson of early stage 1 young.
- D.** Advanced stage 1 young.

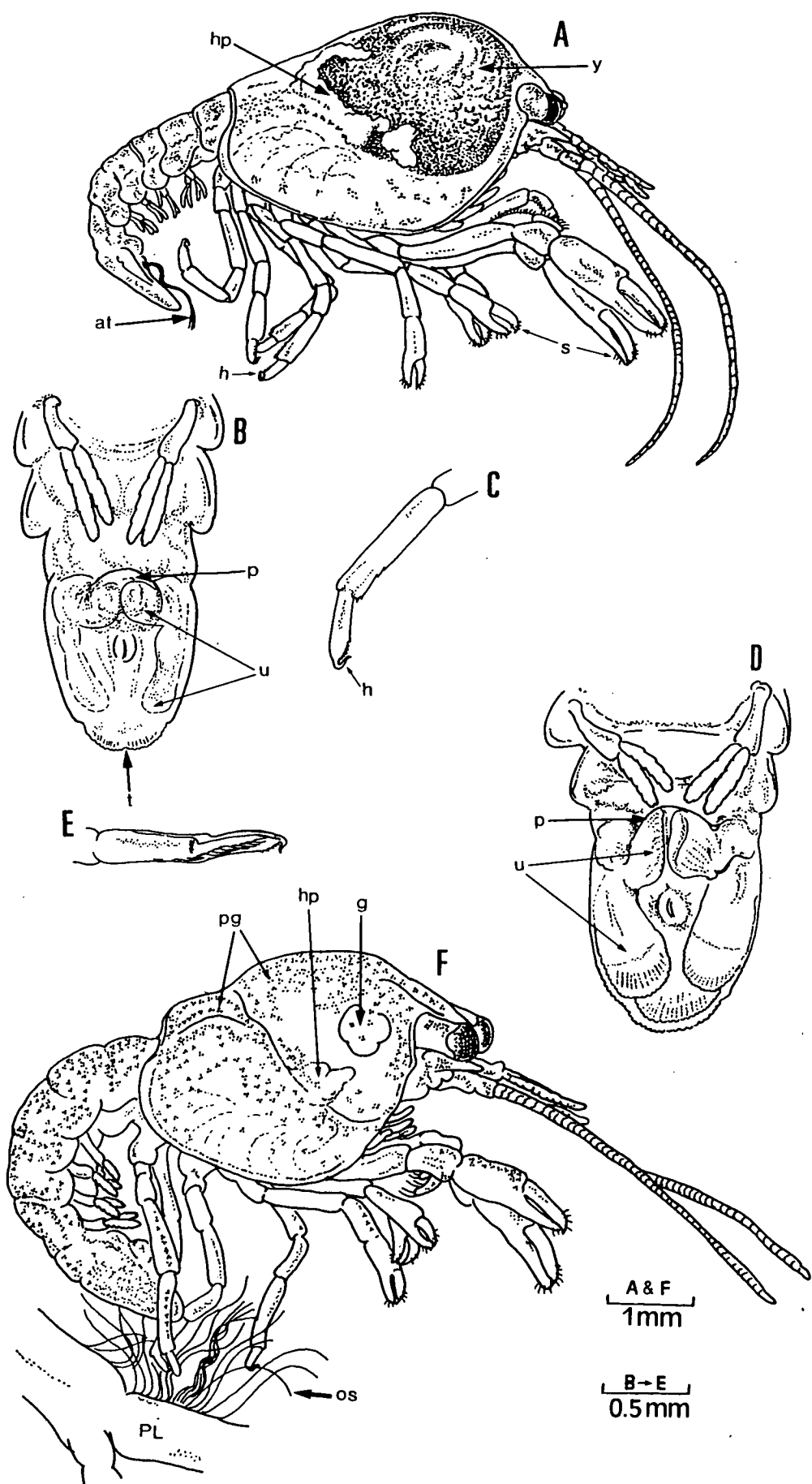


A D
1 mm

B C
0.5 mm

Figure 7.16 Stage 2 young of *Parastacoides t. tasmanicus* from Harlequin Hill, South-West Tasmania:

- A.** Stage 2 young, immediately after moult from stage 1.
- B.** Telson of early stage 2 young.
- C.** Tip of fifth pereopod of early stage 2 young.
- D.** Telson of advanced stage 2 young. Note formation of uropods within papilla.
- E.** Tip of fifth pereopod of stage 2 young just prior to moult. Note new stage 3 pereopod tip within.
- F.** Advanced stage 2 young.



consisting of a large telson with a large papilla containing the developing inner uropodal rami (Fig. 7.16B). Setal buds can be seen on the tip of the telson. A relatively long period of time is spent in this stage (32 to 46 days), and by the time the young is ready to moult to stage 3, several developmental changes can be noted. The advanced stage 2 young is heavily pigmented and has no or little yolk (Fig. 7.16F). Just prior to moulting to stage 3, large gastroliths can be seen in the cephalic region and fully developed uropods can be seen within the large papilla on the tail fan (Fig. 7.16D&F).

Stage 3: As soon as the young moult to stage 3, they become independent of the mothers and begin foraging. There is no sign of an anal thread during the moult and the hooks on the fourth and fifth pereopods are not present in the newly moulted young. The young therefore leave their mothers as they moult out of stage 2. Stage 3 morphology is adult-like, antennae are long, the uropods are completely developed and the body, as well as all appendages including the tail fan, is heavily setose. No sign of gonopore development is evident at this stage. Pigmentation is present on the carapace, abdomen and appendages. Yolk is generally used up in most newly moulted stage 3 young, and food can be detected in the stomach and intestine within days of moulting. The mean carapace length of stage 3 young was 4.20 mm (s.d. = 0.12 , n = 50, range = 3.95-4.35).

Postembryonic development of *P. t. tasmanicus* (I), *P. t. inermis* and *P. t. insignis* is identical to that described for *P. t. tasmanicus* (SP). The main differences are in the size of the young which are smaller in the former three and in the colour of the yolk, which is bright yellow in *P. t. tasmanicus* (I), *P. t. inermis* and *P. t. insignis* but orange-brown in *P. t. tasmanicus* (SP). The diagnostic uropodal spines can first be detected in stage 3 young of *P. t. inermis* and *P. t. insignis*.

7.4 DISCUSSION

Mating, spawning and fertilization:

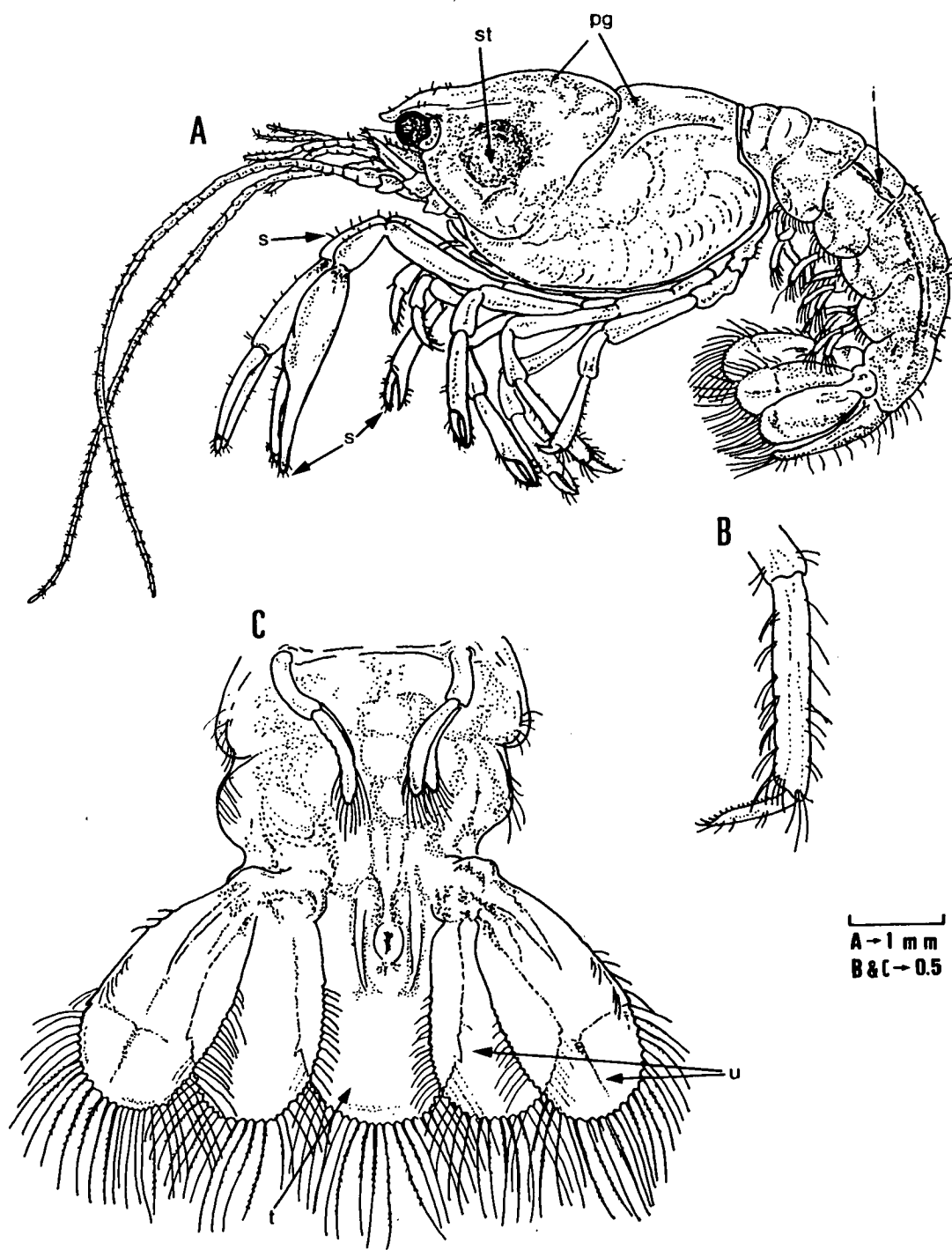
The Parastacidae lack the specialized copulatory structures, such as copulatory stylets and sperm receptacles, found in the Cambaridae, Nephropidae and Astacidae (Hobbs, 1988). The mode of sperm transmission is therefore relatively simple,

Figure 7.17 Stage 3 juvenile of *Parastacoides t. tasmanicus* from Harlequin Hill, South-West Tasmania:

A. Stage 3 young, lateral view. Note absence of yolk and presence of food in digestive track.

B. Tip of fifth pereopod of stage 3 young. Note total absence of recurved spine.

C. Tail fan of stage 3 young.



involving ventral contact between males and females. Females of astacid crayfishes also lack sperm receptacles and, as in the Parastacidae, spermatophores are deposited directly onto the sternum and coxae of the female (Mason, 1970; Ingle & Thomas, 1974). The major difference between the two families lies in the fact that astacid males use their pleopods in sperm transfer, whereas parastacid males extrude sperm directly from their gonopores. In addition, the spermatophores of the Astacidae are short and tubular and their placement also appears more random than in the parastacids (Mason, 1970; Ingle & Thomas, 1974). In the spiny lobsters, which also lack specialized copulatory structures, copulation is very short (a few seconds). It is preceded by courtship and occurs when the male embraces the female venter to venter and deposits a spermatophoric mass onto her sternum (Atema & Cobb, 1980).

The mating behavior, the gross morphology and placement of the spermatophore in other parastacids is similar to that observed in *Astacopsis* and *Parastacoides*. In *Cherax destructor*, courtship occurs prior to mating, copulation may last for up to 15 minutes and involves the female turning on her back and accepting the male on top (Hosking, 1980). The spermatophore is deposited on the sternal keel of the female between pereopods 3 and 4 (Johnson, 1979) and females do not moult prior to mating (Sokol, 1988). In the tropical *C. quadricarinatus*, mating lasts about one minute with the male assuming a supine position underneath the female (Sammy, 1988). The spermatophores of *C. destructor* and *C. tenuimanus* are gelatinous and are deposited on the sternum between the third and fourth pereopods (Shipway, 1951; Johnson, 1979). In *C. destructor* the spermatophore is lost 1 to 2 days after spawning. Turvey (1980) found that the spermatophore of *Euastacus spinifer* was attached to the coxae of the fourth and fifth pereopods and consisted of an amorphous matrix containing highly convoluted tubules with sperm. In the spiny lobsters *Panulirus* and *Palinurus* the spermatophoric mass, consisting of a gel with a protective matrix, is applied to the last two sternal plates (Aiken & Waddy, 1980).

Mating in the Parastacidae is of shorter duration and involves less aggressive behavior than in the Astacidae and Cambaridae, where copulation involves dominant and often aggressive male behaviour and can last up to four hours (Crocker & Barr, 1968; Pippitt, 1977; Berrill & Arsenault, 1982 & 1984). It is highly likely that female parastacids play an important role in determining the exact timing of copulation, since it is crucial for the spermatophores to be deposited just prior to oviposition when

ovaries and glair glands are ready to extrude their contents. Aggressive behavior during mating would not be advantageous as it would make the deposition of spermatophores difficult, less accurate with respect to placement and could even result in the total loss of the spermatophore.

Astacopsis females moult well prior to mating/spawning (60 days) while *Parastacoides* females moult shortly before mating (10 to 14 days). Copulation occurs after the female has hardened although in *Parastacoides*, mating females are still semi-soft following the recent pre-reproductive moult. Pairing in *Parastacoides* appears to occur just prior to or just following the female moult. It is therefore likely that it is the males that search out the burrows of reproductive females using pheromones given off during moulting as a cue to find potential mates. Indeed, no males mated with or were found in burrows with nonreproductive females, suggesting that there must be an efficient recognition mechanism of the reproductive condition. During the mating season, several males were found in the top passages of burrows suggesting searching activity. Some burrows in which mating pairs were found still contained some juveniles from the female's last brood. Other studies have shown that chemical communication in crayfish can enable recognition of sex, condition and as species (Tierney & Dunham, 1982 & 1984; Hazlett, 1985). Similarly, females of the lobster *Homarus americanus* release a sex pheromone before moulting and mating (Atema, 1986). Females of this species have been observed seeking out, courting (by pheromone release) and taking up residence with males several days before moulting. Mating takes place about 30 minutes after moulting and males then guard the softshelled females until they harden. Given the short period between mating and spawning, it is possible that similar guarding may occur in *Astacopsis* and *Parastacoides*. Males may stay with females (after copulation) until the latter have spawned, thus ensuring that the females are not disturbed or mated with again.

In *Parastacoides* mating pairs, males are generally larger or of the same size as the females, suggesting some form of sexual selection or competition may be operating. The copulating males are generally large, (CPL \geq 31 mm) suggesting that small reproductive males are excluded from copulation either by female selection or by competition with larger males. Since the male to female ratio is approximately one to one (see Chapter 8) and only half of the adult females in a given population mate each season, there must be a surplus of available males, thus making competition for

mates likely. The presence of more than one male in a female's burrow shows that males come into contact with each other during the mating season, and further supports the possibility of competition and/or selection. Intense inter-male competition during the mating season has been documented in astacid and cambarid crayfishes, with large males mating more successfully than smaller males (Stein, 1976; Berrill & Arsenault, 1984; Woodlock & Reynolds, 1988).

Spawning in the Parastacidae must take place immediately following copulation, as long term sperm storage is impossible due to the lack of organs for sperm storage in females. In the Cambaridae and Nephropidae where a sperm receptacle is present the period between mating and spawning is considerably longer, in some cases lasting up to many months (Crocker & Barr, 1968; Aiken & Waddy, 1980). In the Astacidae, where sperm storage organs are also absent, spawning takes place from a few days to several weeks after mating (Cukerzis, 1988).

Parastacid eggs are probably fertilized when they pass over the spermatophore on their way to the abdominal egg chamber. The spermatophore is partly dissolved away at this time and sperm is probably released as the eggs and associated fluids flow over the spermatophore. A similar external fertilization mechanism has been proposed for spiny lobsters (Aiken & Waddy, 1980). Crocker and Barr (1968) stated that in the Cambaridae, sperm is released from the receptacle into the glair, and fertilization occurs in a "water free environment". Other authors have hypothesized that the spermatophore of *Astacus* and *Pacifastacus* is dissolved by the glair gland secretions (Mason, 1970; Holdich & Reeve, 1988; Cukerzis, 1988). This does not appear to be the case in *Astacopsis* and *Parastacoides* as the glair is enclosed within the brooding chamber and may not be released until some time after spawning.

The sequence of spawning behaviour observed in *Astacopsis* is similar to that described in other Astacidea (Mason, 1974; Ingle & Thomas, 1974; Aiken & Waddy, 1980). The spawning stance and subsequent turning is most similar to that described for *Pacifastacus trowbridgii* (Mason, 1970). In the Parastacidae, spawning has been previously described only in *Cherax destructor* (Lewis, 1976; Johnson, 1979; Mills, 1983). Females of this species spawn on their back or side, turning periodically. As in *Astacopsis*, the eggs are held in a tightly cupped abdominal brood chamber into which glair is secreted.

The secretion of glair during spawning has been documented in numerous astacid and cambarid crayfishes as well as in various marine lobsters (Yonge, 1937;

Crocker & Barr, 1968; Mason, 1970; Ingle & Thomas, 1974, Aiken & Waddy, 1980). This substance has also been credited as being instrumental in egg attachment (Yonge, 1937, Stephens, 1952; Holdich & Reeve, 1988). Glair secretion in the Tasmanian parastacids takes place either during or following egg extrusion but cannot be observed because of the tightly cupped abdomen. Traces of glair can however be seen in egg stalks and on abdomens of recently spawned individuals. Egg attachment probably occurs during the turning behavior and appears to take up to several days. Disturbance of the egg chamber at this time invariably results in loss of the brood, apparently due to the failure of eggs to attach. The uncupping of the abdomen breaks the tight seal and probably results in the leaking of the contents and may also disturb the chemical balance of the glair-ova solution. The sealed abdominal brood chamber appears to be characteristic of parastacid reproduction.

It is possible that glair in the Parastacidae is produced in smaller amounts, or is chemically different from that of the Astacidae and Cambaridae. Indeed the extruded glair in the northern hemisphere crayfishes is thick, mucoid and surrounds the eggs in a protective apron (Crocker & Barr, 1968; Mason, 1970; Ingle & Thomas, 1974). The formation of this apron does not occur in the parastacids and the solution within the cupped tail fan is rather clear and fluid.

Eggs are attached to the ovisetae on the pleopods of the female. The egg stalks are made up of several twisted ovisetae stuck together by a globular substance presumed to be the glair secretion. The tips of the oosetae are in turn embedded into the outer egg capsule. Several investigators have stated that the outer egg membrane and the egg stalks in crayfishes and lobsters are formed from the solidified glair secretion (Yonge, 1937; Crocker & Barr, 1968; Holdich & Reeve, 1988). The mode of attachment was identical to that described in other Parastacidae (Clark, 1937; Hopkins, 1967A; Suter, 1977; Johnson, 1979) as well as Cambaridae, Astacidae, Nephropidae and Palinuridae (Huxley, 1880; Yonge, 1937; Crocker & Barr, 1968; Aiken & Waddy, 1980; Holdich & Reeve, 1988).

Embryonic and postembryonic development:

The embryonic development was identical in *Astacopsis* and *Parastacoides* and corresponded to that described in *Cherax destructor* (Johnson, 1979) and *Astacus fluviatilis* (Huxley, 1880). The early larval stages are entirely embryonized and young hatch as stage 1 juveniles. The hatching process was identical to that

described in *Orconectes* and *Pacifastacus* by Andrews (1907). The change in the yolk colour during egg development has been noted in the eggs of *Paranephrops planifrons* (Hopkins, 1967A). The change in the colour of the yolk parallels embryonic development and can therefore be used as a reliable and quick indicator of development in the field.

Early postembryonic development has previously been described in a varying degree of detail in several parastacid, astacid and cambarid crayfish species (Huxley, 1880; Andrews 1907; Clark, 1937; Hopkins, 1967A; Crocker & Barr, 1968; Suter, 1977; Johnson, 1979; Price & Payne, 1984; Rudolph & Rios, 1987; Köksal, 1988; Holdich & Reeve, 1988). The development sequence consists of 3 stages (attained in 2 moults) with stages 1 and 2 being attached to the mother and having a large yolk mass and undifferentiated tail fan, and stage 3 having a fully differentiated tail fan and displaying varying amounts of independence. Felder *et al.* (1985) provided a general overview of postlarval development in the Decapoda and pointed out the importance of early postlarval development in further resolving relationships between decapod taxa.

The general development sequence from stage 1 to stage 3 in *Astacopsis* and *Parastacoides* was similar to that described in the above mentioned studies, but several major differences were found. The main differences between the two genera were that *Astacopsis* underwent 3 moults during its development before becoming independent as a late stage 3, while *Parastacoides* underwent the usual 2 moults after hatching but became independent immediately upon moulting to stage 3. Freshly hatched stage 1 young were initially attached to the egg case by a telson thread formed from the inner lining of the egg capsule. Similarly, Andrews (1907) found the telson thread of *Orconectes limosus* was short and made of the inner egg capsule membrane while that of *Pacifastacus leniusculus* was long and made of the cast off embryonic skin. The presence of this telson thread has been previously noted in other parastacid, astacid and cambarid species and appears to be universal among freshwater crayfishes. The telson margin of stage 1 parastacids is smooth and bears no special structures for the attachment of the telson thread seen in the Astacidae and Cambaridae (Andrews 1907; Price & Payne, 1984; Holdich & Reeve, 1988). The presence of the anal thread in the Parastacidae has not been previously documented. Andrews (1907) described the anal thread and its function in *Orconectes limosus* but no other references to this structure exist in other studies of crayfish early

development. The anal thread was noted in all "larval" moults in *Astacopsis* but in *Parastacoides* it occurred only in the stage 1 to stage 2 moult. The absence of this structure in the stage 2 to stage 3 moult can be explained by the fact that stage 3 young are wholly independent from their mothers and therefore do not need to maintain contact with them. The occurrence of a papilla on the telson has been recorded in several parastacids (Suter, 1977, Fig. 1b; Johnson, 1979). This study clearly shows that the papilla contains the forming inner rami of the uropods and disappears as soon as the tail fan is differentiated externally. It is not clear whether similar uropod development also occurs in the Cambaridae and Astacidae.

The major difference in early development between the Parastacidae and the Astacidae-Cambaridae is the mode of attachment of the first and second stage young. The parastacid young have a specialized recurved spine and associated hooklets on the dactylus of the fourth and fifth pereopod. These spines clip onto the oosetae and as a result the young hang upside down from the female's pleopods. In contrast, the stage 1 and 2 young of the Cambaridae and Astacidae have hooked tips on the fingers of their chela by which they cling to their mother. Gurney (1935) considered this character to be strong evidence that the northern hemisphere and the southern hemisphere crayfishes have become independently adapted to fresh water. This view has to be approached with caution because of some similarities in development between the two groups such as the general similarity of the larval stages as well as presence of telson and anal threads.

Parastacoides and *Astacopsis* have therefore markedly different early life histories, with the former undergoing fewer moults and becoming independent at an earlier stage in development. Such abbreviated dependence on the mother also occurs in several South American burrowing species of *Parastacus* (Rudolph & Zapata, 1986; Rudolph & Rios, 1987) as well as in the Astacidae where young are completely independent by stage 3 (Andrews, 1907; Arrignon, 1981; Köksal, 1988; Cukerzis, 1988). In other parastacids such as *Euastacus*, *Paranephrops*, *Engaeus* and *Cherax* the three juvenile stages are similar to those seen in *Parastacoides* but remain dependent on their mothers until late stage 3 (Hopkins, 1967A; Suter, 1977; Johnson, 1979; Turvey, 1980).

The postembryonic development in *Astacopsis* appears to be significantly different from other parastacids as well as astacids and cambarids. The young undergo three moults during their development resulting in four morphologically

distinct stages: early stage 1, late stage 1, stage 2 and stage 3. Stage 2 young have a differentiated tail fan but the uropods are short and without setae. Early stage one is embryonic in morphology and of very short duration and it appears that the first moult is actually the shedding of the embryonic cuticle. Similarly, Andrews (1907) noted that the embryonic cuticle in *Pacifastacus* is shed during hatching and serves as the anal thread. This type of development reflects the ancestral condition in the Astacidea, assuming that the ancestor of freshwater crayfishes had larval development similar to present day nephropid lobsters. Larval development in the Nephropidae is brief when compared to other Decapoda, involving only three pelagic larval stages and a fourth, initially pelagic then benthic, fully developed postlarva (Gurney, 1960; Phillips & Sastry, 1980; Aiken & Waddy, 1986). Andrews (1907) proposed that stages 1 to 3 in the marine lobster were comparable to stages 1 and 2 in freshwater crayfishes while he considered the fourth stage of the lobster and the third stage of the crayfish homologous on the basis of morphological and behavioral characters. From this he concluded that "the process of reduction of metamorphoses that has already gone so far in the lobster, has advanced a little more in the crayfish so that only two larval stages exist where there used to be three". The evolution of crayfish from marine ancestors presumably involves, in the larval stages, the loss of adaptations for pelagic life and the acquisition of adaptations for dependence on the mother. The early development of *Astacopsis* can therefore be considered primitive in having retained some of the ancestral larval characters, in particular the 4 developmental stages, and early differentiation of swimming appendages in the form of the tail fan. The number of development stages in *Astacopsis* and the related marine lobster *Homarus* are therefore identical and the general morphology of the stages are similar, with the tail fan becoming differentiated after the second moult but adult-like morphology not being attained until the third moult. Since such development apparently does not occur in other parastacids it appears that *Astacopsis* is an ancient genus with primitive characters which has branched from the parastacid line early in the evolution of the family. Indeed, on the basis of electrophoretic and morphological characters, the genus has been considered by some authors to be more ancestral than many parastacids (Smith, 1912; Patak & Baldwin, 1984). The very large size, long breeding cycle and life span seen in *A. gouldi* are also reminiscent of the ancestral marine life style.

Given this new information it is proposed that freshwater crayfish larval

development recapitulates the entire primitive decapod sequence of larval stages: the nauplius to first zoea phases are embryonized, stages 1 and 2 correspond to the late zoea larval stages and the young become independent in stage 3 as postlarvae, homologous to the settling fourth stage seen in *Homarus*. The view that stage 3 young of crayfishes should be considered as postlarvae rather than third zoeas as proposed by Andrews (1907) seems reasonable given the fact that stage 3 young lose all of the special adaptations related to life on their mothers.

CHAPTER 8 : GROWTH / POPULATION DYNAMICS

8.1 INTRODUCTION

Freshwater crayfishes grow by periodically shedding their highly calcified exoskeleton. This process is called moulting or ecdysis. Prior to moulting some of the calcium from the old carapace is taken up via the haemolymph and stored in a pair of gastroliths in the epithelium of the cardiac portion of the stomach (Aiken & Waddy, 1987; Lowery, 1988). After ecdysis is complete, the gastroliths are redissolved into the new exoskeleton thus speeding up the hardening process. Further calcium recovery is accomplished by consuming the shed exoskeleton.

The overall growth of crayfishes depends on the frequency of moulting and the growth increment in each of the moults. The frequency of moulting and the moult increment are influenced by various environmental factors such as water temperature and quality, food availability and population density (Aiken & Waddy, 1987). Moulting activity is therefore strongly seasonal, generally occurring from spring to autumn, when water temperatures are relatively warm and nutrients are abundant. The frequency and increment also vary according to on the size/age, reproductive condition and sex of an individual (Hopkins, 1967B, Prins, 1968; Pratten, 1980; Arrignon, 1981; Hamr & Berrill, 1985; Aiken & Waddy, 1987; Lowery, 1988).

Although the genus includes the largest freshwater crayfish in the world, neither the growth nor population biology of *Astacopsis* have hardly been studied to date. Forteach (1985), in an unpublished laboratory study of the aquaculture potential of *Astacopsis gouldi*, found that the growth rate was slow and the moult frequency decreased with increase in body size. Similarly, there is little known about growth and population structure in *Parastacoides*. Lake and Newcombe (1975) provided some information on population structure and density but did not examine growth in their ecological study of *P. t. tasmanicus*. In the only other growth-related study, Mills and Lake (1975) devised a moult staging scheme based on the development of setae of the tail fan of *P. t. tasmanicus*.

This chapter examines the growth, moulting frequency and increment as well as structure and density in selected populations of *Astacopsis gouldi*, *A. franklinii* and

P. t. tasmanicus.

As the main aim of this study was to compare the reproductive biologies of the three species, moulting and growth were examined only as a part of the detailed study of their reproductive cycle. For the sake of brevity, the treatment of the data obtained was preliminary rather than exhaustive.

8.2 METHODS

The monthly catchability and activity estimates were obtained from catches in monthly samples for each species. Sex ratios were obtained by comparing the numbers of males and females in monthly and total catches. Size frequency histograms were constructed from carapace length measurements taken during monthly samples. Frequency distributions of *A. gouldi* from the Dip and Detention rivers were combined as the two rivers were similar and at close proximity (additionally, the samples taken were relatively small due to the remoteness of the sites).

The population density of each species was estimated from the capture recapture data using the Lincoln Index, a method which has been used in previous ecological studies of freshwater crayfishes (Woodland, 1967; Lake & Sokol, 1986):

$$N = M (C + 1) / R + 1$$

where N = estimate of total number of crayfish in population, M = total number of crayfish marked and released, C = number of different crayfish in each census sample, and R = number of recaptures.

Absolute growth rates for *A. gouldi* were calculated as change in carapace length since last capture divided by months since last capture.

The moulting process and behaviour was described by examining crayfishes in the laboratory prior to, during, and after ecdysis.

The seasonal moulting cycle of adult and juvenile crayfish of both sexes was described by assessing the moulting condition of each crayfish captured throughout the year. Crayfish were classified according to the condition of their exoskeleton into the following categories: 1. hard and dirty, 2. hard and clean, 3. buster (crayfish about to moult showing distinct separation of thorax and abdomen as well as general decalcification), 4. softshell (crayfish just moulted exoskeleton completely soft, and

5. semi-soft/recently moulted. The presence of gastroliths which could be seen through the carapace in field collected pre- and post-moult animals was also noted and preserved crayfishes were checked for gastrolith formation during dissection.

The moult frequency and growth increments per moult were obtained from capture-recapture field experiments as well as from animals kept in the laboratory. The monthly growth of *Parastacoides* juvenile broods were estimated from field measurements taken during the regular sampling schedule.

A number of males and females of each species were kept in the laboratory from spring to autumn to gain information on seasonal growth rates of various size classes of crayfish. Temperature and photoperiod were kept at seasonal levels and crayfish were provided with a natural diet as well as small pieces of fish flesh. During periods of increased moulting activity in the field, crayfish in the buster condition were brought into the laboratory and were kept in aquaria until they moulted. Their new body dimensions were then remeasured to gain information on growth of various body parts.

Annual growth rates of various size classes of crayfishes were calculated by multiplying the average size increment per moult by the number of moults undergone in a growing season (spring to autumn). Absolute growth rates (after Lake & Sokol, 1986) were calculated as the change in carapace since last capture divided by months or days since last capture. Estimates of age at various sizes were made by dividing the carapace length by the mean annual growth rate.

8.3 RESULTS

A. POPULATION DYNAMICS

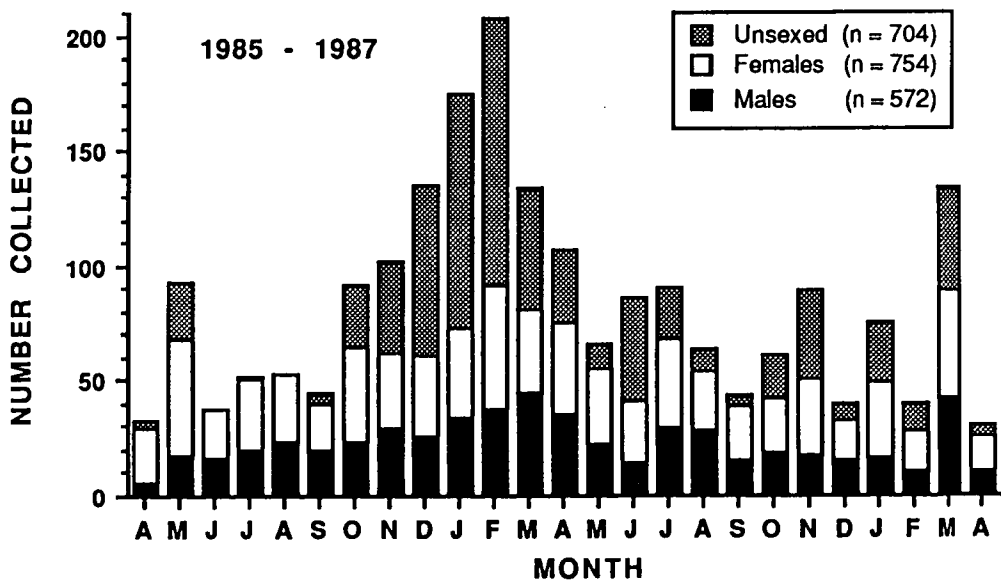
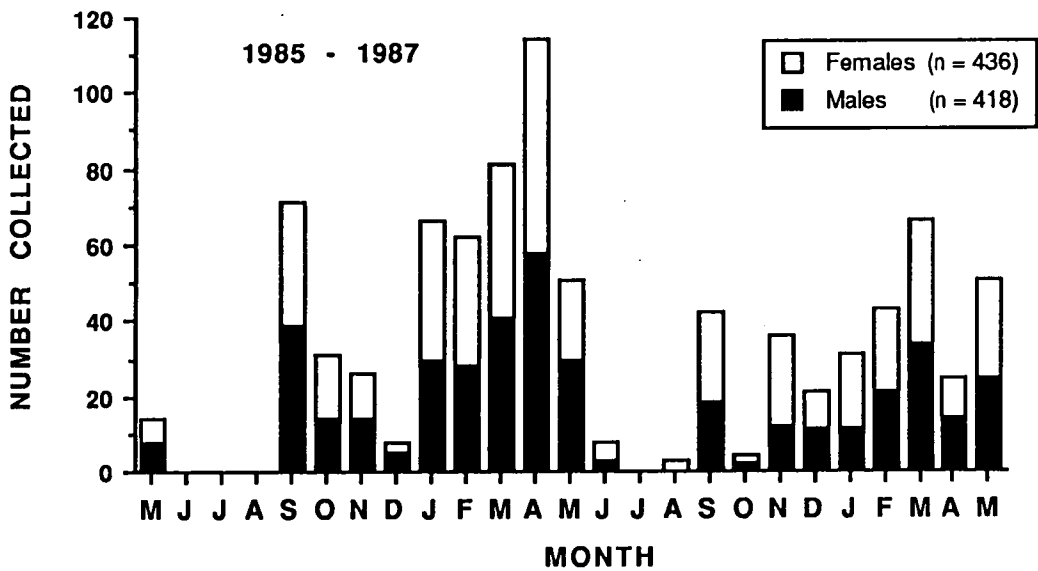
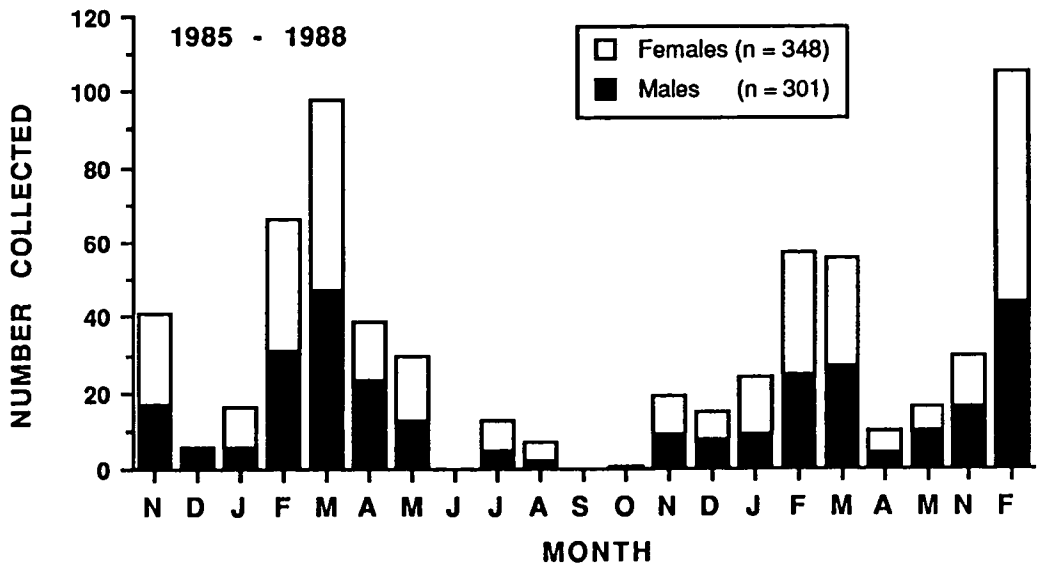
8.3.1 Monthly catchability

Astacopsis gouldi: The number of crayfishes in monthly samples from the Inglis River sampling site is shown in Figure 8.1. The numbers caught generally reflected the activity level of the crayfishes. Crayfishes were most active in late summer (February and March) when they were seen walking and foraging in the open. In contrast, during the winter months, crayfish were relatively inactive and were not seen in the open.

Figure 8.1 Number of males and females of *Astacopsis gouldi* captured in monthly samples from November 1985 to May 1987 in the Inglis River. (Note: two additional samples were taken in November 1987 and February 1988).

Figure 8.2 Number of males and females of *Astacopsis franklinii* captured in monthly samples from May 1985 to May 1987 in Hobart and Guy Fawkes Rivulets (combined data).

Figure 8.3 Number of males, females and unsexed juveniles of *Parastacoides t. tasmanicus* captured in monthly samples from April 1985 to April 1987 at the Harlequin Hill sampling site.



Astacopsis franklinii (Eastern form): The number of crayfishes caught monthly at the Mt Wellington sampling sites is shown in Figure 8.2. As in *A. gouldi*, the numbers caught generally reflected the activity levels of the crayfishes. Crayfishes were most active in late summer (March and April) when they were seen walking and foraging in the open. In March, it was common to see several adults foraging in the leaf litter or on submerged wood in large pools.

Parastacoides t. tasmanicus (SP): The number of crayfishes captured monthly at the Harlequin Hill sampling site is shown in Figure 8.3. Unlike in *Astacopsis* the numbers did not correspond to the activity of the crayfish but rather reflected the sampling intensity as well as the effort required to obtain crayfish. Burrows were more difficult to dig out during the winter months due to cold temperatures, high water levels and waterlogging of the soil. Activity of crayfishes was therefore estimated from the pitfall trap catches as shown in Figure 8.4. The largest catches per night were obtained generally from late winter to spring while the lowest occurred in mid summer when surface water temperatures were high and water levels were low.

8.3.2 Sex ratio

Astacopsis gouldi: The mean monthly male to female ratio (ie: F/M) of all size classes in the Inglis River population was 1.22 (s.d. = 0.51, range 0.2 - 2.5, n = 18). Overall, the ratio in the total number of crayfishes collected over the two year period was 1 : 1.16 in favour of females. This difference in number between the sexes did not constitute a significant departure from the expected 1:1 ratio ($\chi^2 = 1.6$, d.f. = 1, $p < 0.1$).

The male to female ratios in other *A. gouldi* populations were as follows: 1 : 0.98 at Dip River (n = 52); 1 : 0.96 at Big Creek (n = 104), 1 : 0.78 at Detention River (n = 16).

Astacopsis franklinii (Eastern form): In combined samples from Hobart and Guy Fawkes Rivulets the mean monthly male to female ratio of all size classes was 1 : 1.09 (s.d. = 0.37, range 0.6 - 2.0, n = 20). Overall the ratio in the total number of crayfishes collected from the two streams over the two year period was 1 : 1.04 in favour of females (n = 649). This difference in number between the sexes did not constitute a significant departure from the expected 1:1 ratio ($\chi^2 = 0.19$, d.f. = 1,

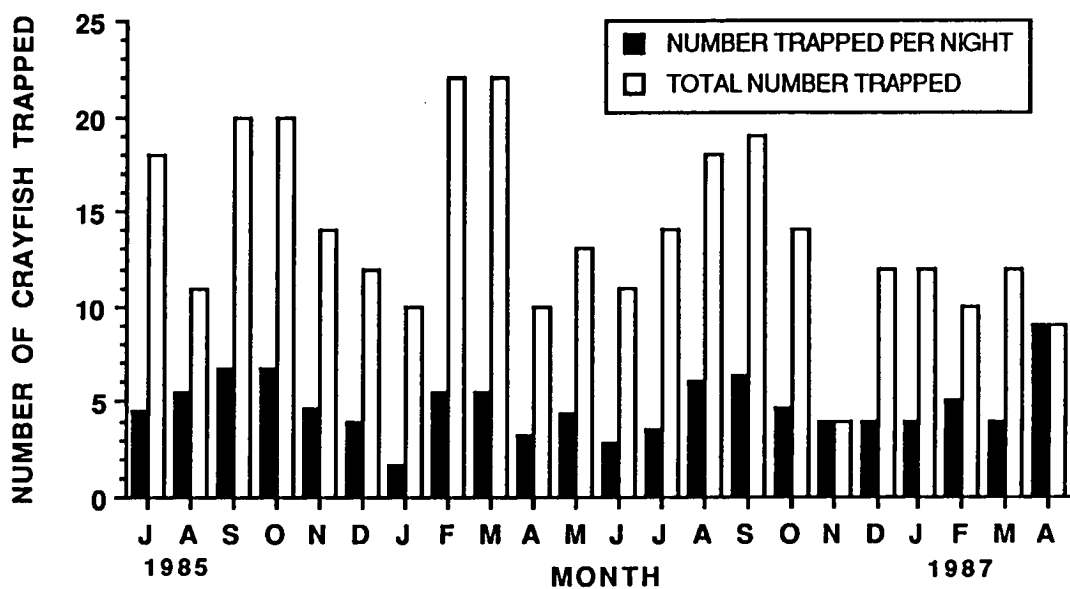


Figure 8.4 Number of *P.t.tasmanicus* captured in the pitfall traps at Harlequin Hill between July 1985 and April 1987. The open histograms represent the total number of crayfish captured each month while the solid histograms represent the average number of crayfish captured per night each given month.

$p < 0.9$).

Astacopsis franklinii (Western form): In the combined samples from all sampling sites over the two year period, the male to female ratio was 1 : 0.93 ($n = 854$).

Parastacoides t. tasmanicus (SP): In the Harlequin Hill population, the mean monthly male to female ratio (all size classes) was 1 : 1.55 (s.d. = 0.61, range 0.93 - 3.83, $n = 25$). Overall the ratio in the total number of crayfishes collected over the two year period was 1 : 1.32 in favour of females ($n = 1326$). This difference in number between the sexes constituted a significant departure from the expected 1:1 ratio ($\chi^2 = 12.5$, d.f. = 1, $p < 0.001$).

Other *Parastacoides*: The overall male to female ratio was 1 : 2.05 in *P. t. tasmanicus* (N) ($n = 58$), 1 : 1.3 in *P. t. inermis* ($n = 81$) and 1 : 2.5 in *P. t. insignis* ($n = 32$).

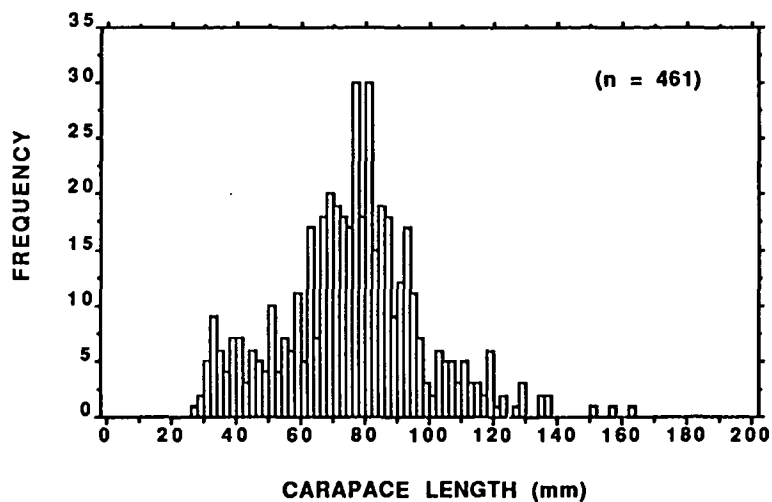
8.3.3 Size frequencies

Astacopsis gouldi: Figure 8.5 shows the polymodal size frequency distribution of the Inglis River population. Most animals captured were in the 60 to 90 mm CPL range. The numbers of the very small juveniles as well as breeding-size adults were conspicuously low. This appears to be, at least in part, the result of heavy fishing pressure on this population (see Appendix 1). The carapace length range of males captured at this site was 29.7 - 151 mm while in females the range was 26.7 - 163 mm.

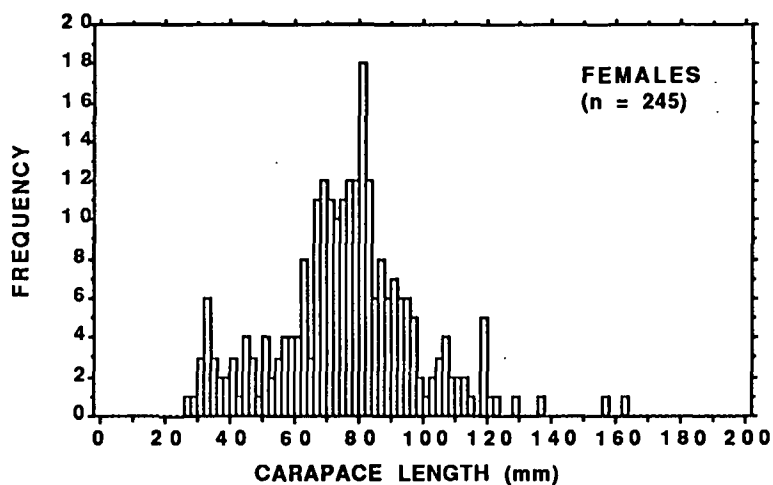
Figure 8.6 shows the overall size frequency distributions of all *A. gouldi* captured at various sites during this study as well as another three populations which were sampled as secondary sites during this study. The Big Creek population, which was heavily fished in some areas, had a larger proportion of small individuals and a somewhat more even size distribution than the Inglis River population but large adults were still low in number. Crayfishes caught at this site ranged in carapace length from 11.0 to 180.0 mm. The Dip-Detention River sites, which were remote and therefore relatively undisturbed, had larger proportions of small individuals and a more even distribution of the medium to large size classes. Crayfishes caught at these sites ranged in carapace length from 15.4 to 199.5 mm.

Astacopsis franklinii (Eastern form): Figures 8.7 and 8.8 show the size

A.



B.



C.

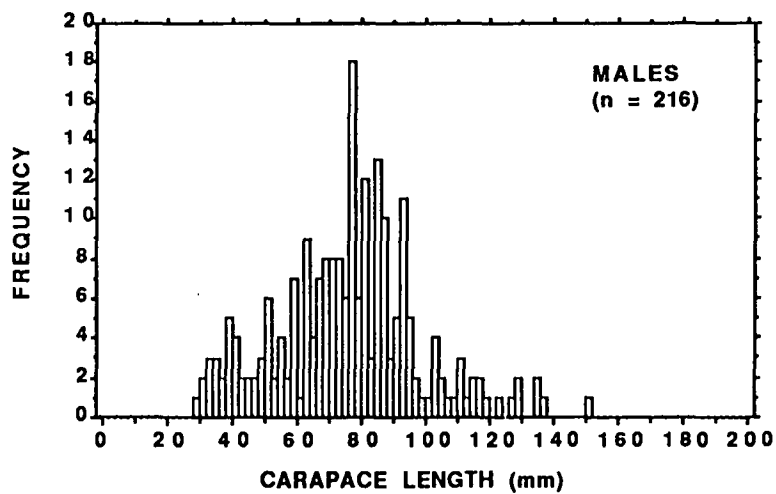


Figure 8.5 The size frequency distribution of *Astacopsis gouldi* collected from November 1985 to February 1988 from the Inglis River population: **A.** All crayfishes; **B.** Females; **C.** Males.

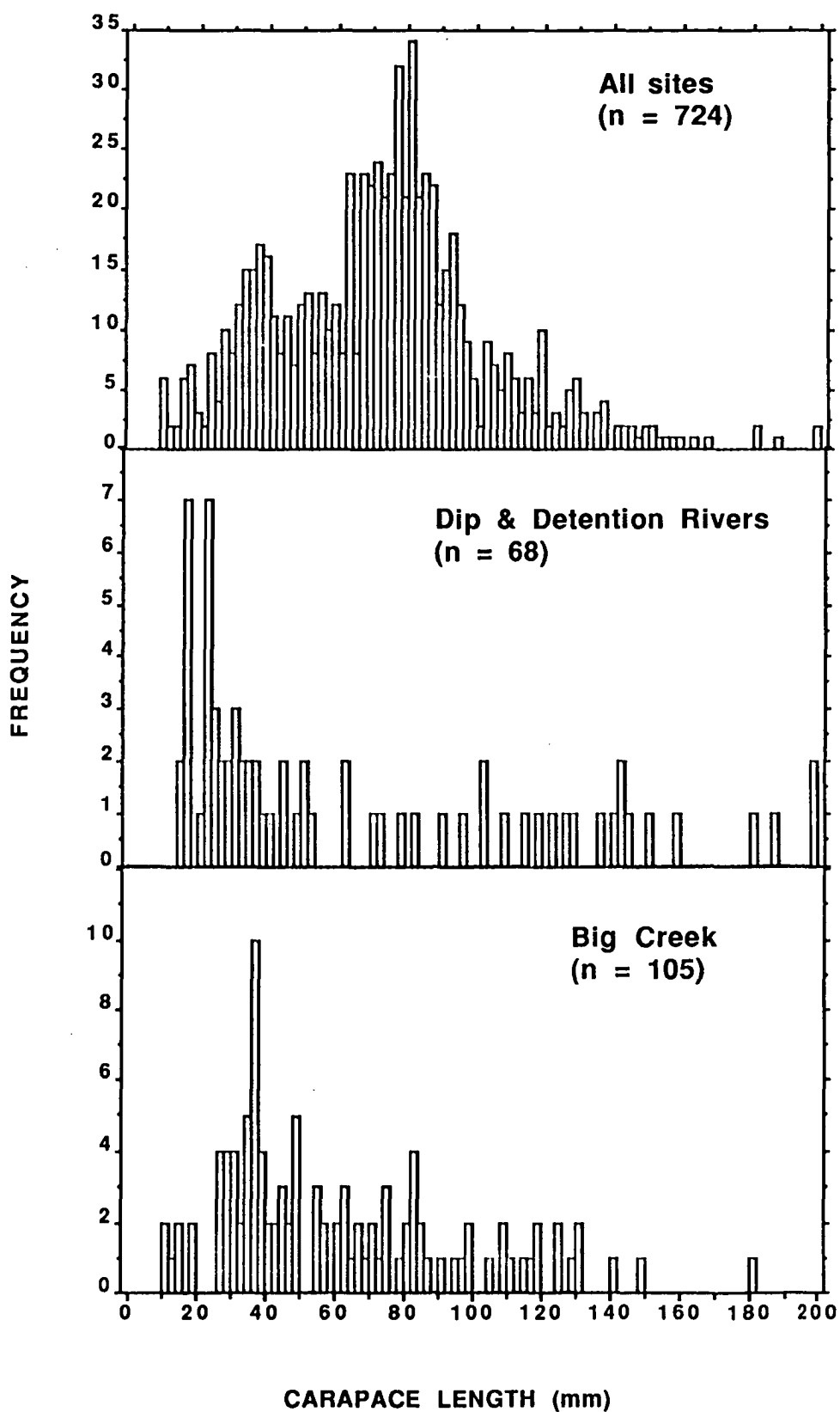


Figure 8.6 The size frequency distribution of *Astacopsis gouldi* collected from various populations from 1985 to 1988.

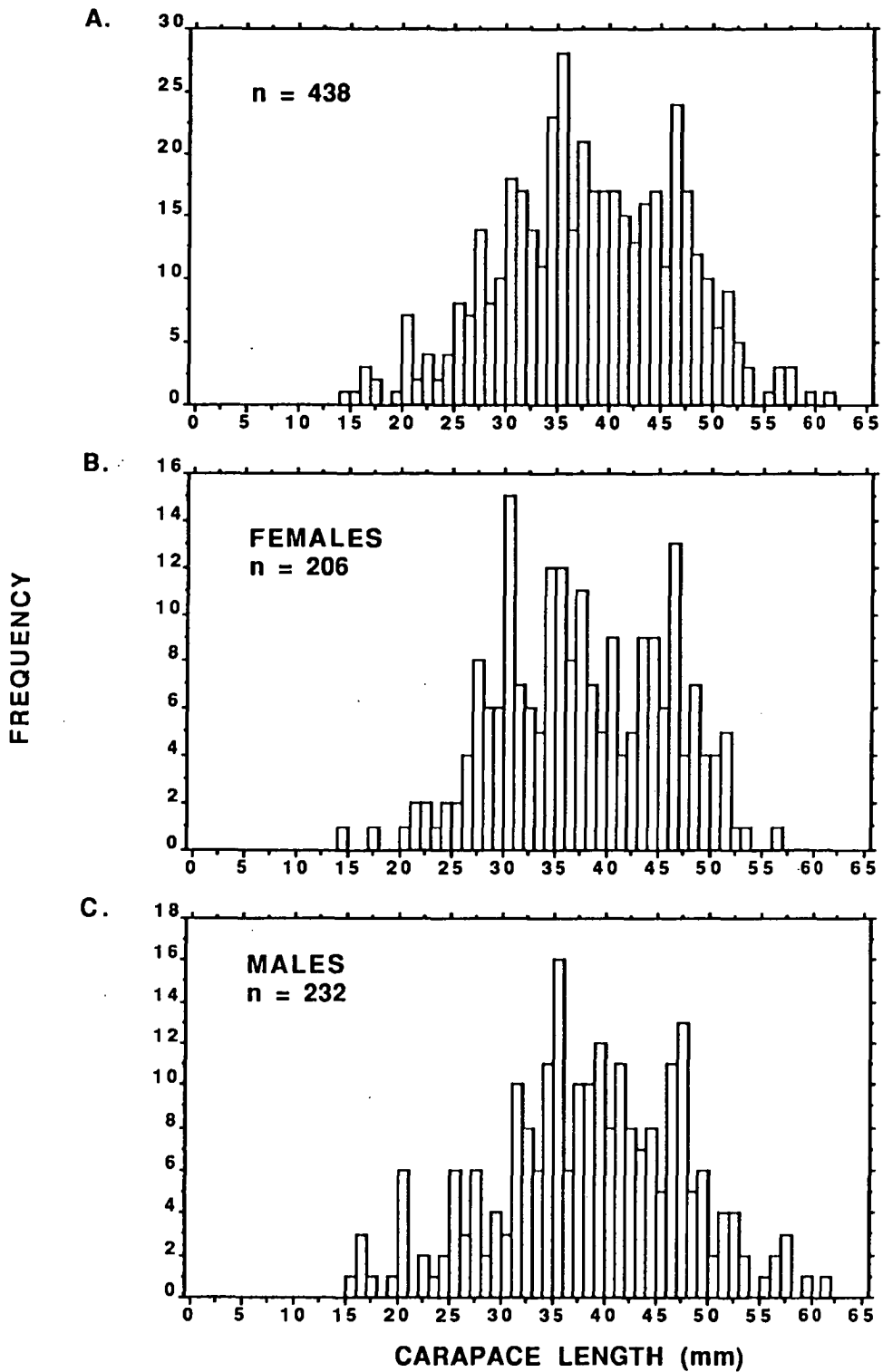


Figure 8.7 The size frequency distribution of *Astacopsis franklinii* (Eastern form), collected from September 1985 to May 1987, in Hobart Rivulet, Mt. Wellington:

A. All crayfishes; **B.** Females; **C.** Males

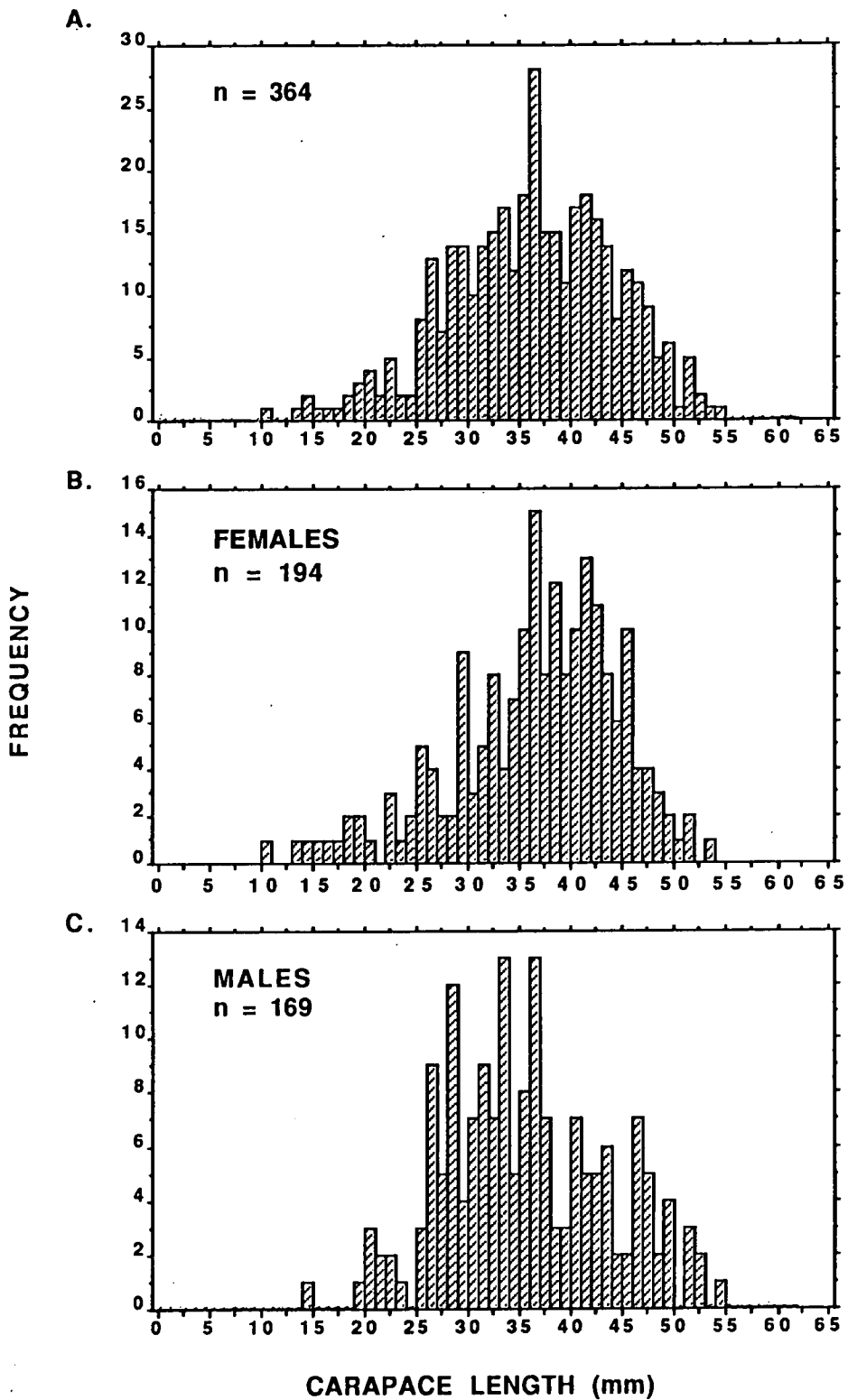


Figure 8.8 The size frequency distribution of *Astacopsis franklinii* (Eastern form), collected from September 1985 to May 1987, in Guy Fawkes Rivulet, Mt. Wellington:

A. All crayfishes; **B.** Females; **C.** Males

frequency distribution of the crayfishes captured in the Mt. Wellington stream populations. The low numbers of small juveniles in both rivulets resulted from the difficulty of catching these very small individuals which apparently burrow deep into the gravel stream bed soon after leaving their mothers. The average carapace length of captured individuals was 37.8 mm (range: 14.5 - 61 mm) in Hobart Rivulet and 35.9 mm (range 10.5 - 54) in Guy Fawkes Rivulet. Overall, the carapace length range of males captured at the two sites was 14 - 61 mm while in females it was 10.5 - 56 mm.

Astacopsis franklinii (Western form): Figure 8.9 shows the size frequency distribution of crayfishes caught at the Clarence Lagoon sampling site. The average carapace length of captured individuals was 57.8 mm with a range of 18 - 90.5 mm. The absence of the smaller size classes of crayfishes is due to the difficulty of obtaining small specimens in deep water in this lake population.

Parastacoides t. tasmanicus (SP): Figure 8.10 shows the size frequency distribution of crayfishes caught at the Harlequin Hill sampling site. As for the *Astacopsis* species, the distribution exhibited polymodality characteristic of long lived seasonal breeders. The size frequency distribution of the population was characterized by very large numbers of very small juveniles, moderate numbers of immatures and relatively large numbers of adults. The average carapace length of sexed individuals was 25.2 mm and the carapace length range was 12 - 35.5 mm in males and 12.4 - 35 mm in females.

Other *Parastacoides*: Figure 8.11 shows the size frequency distribution of *P. t. tasmanicus* (N) caught at the Needles Range sampling site. The size frequency distribution was similar to that of *P. t. tasmanicus* (SP) with the average carapace length of sexed individuals being 25.9 mm (range: 11.5 - 33.6 mm).

Figure 8.12 shows the size frequency distribution of *P. t. inermis* caught at the Harlequin Hill sampling site. *P. t. inermis* of both sexes were generally smaller than *P. t. tasmanicus* (SP) and (N) with an average carapace length of sexed individuals of 19.4 mm (range: 10.0 - 29.0 mm).

8.3.4 Population density

Astacopsis gouldi: In the Inglis River, population size estimates were obtained from monthly capture-recapture data. Overall, in the 750 meters of river

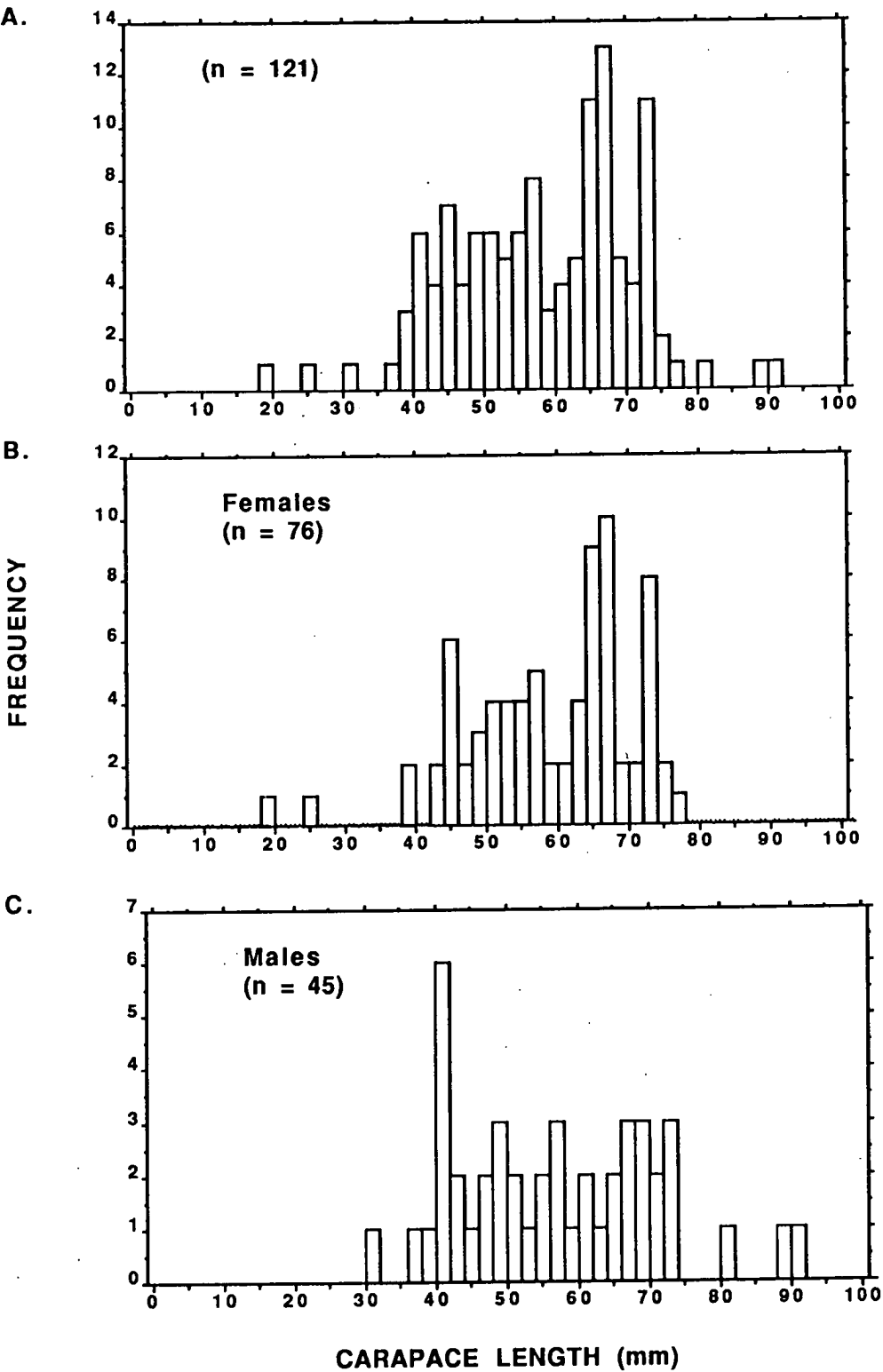
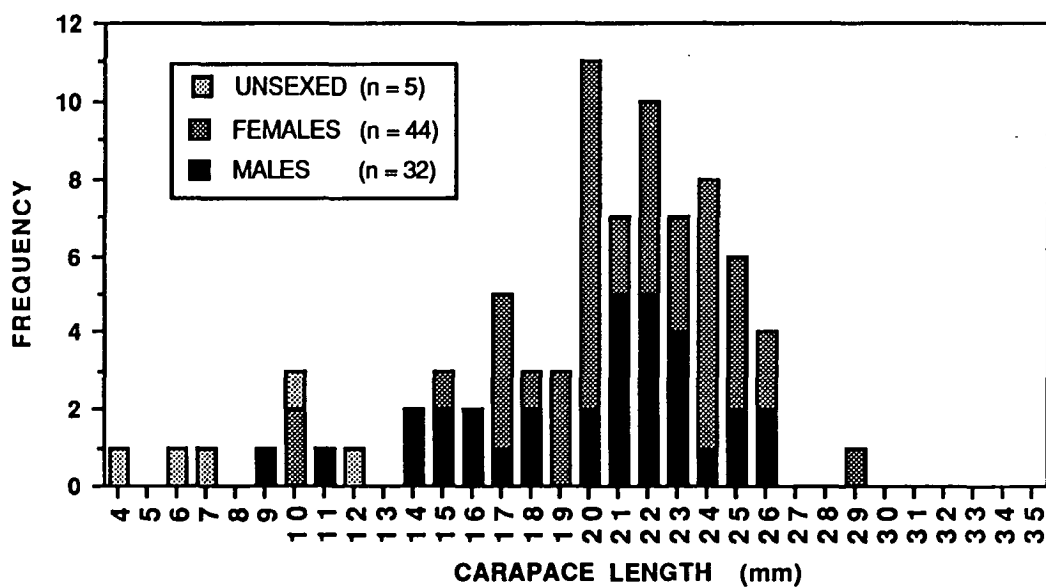
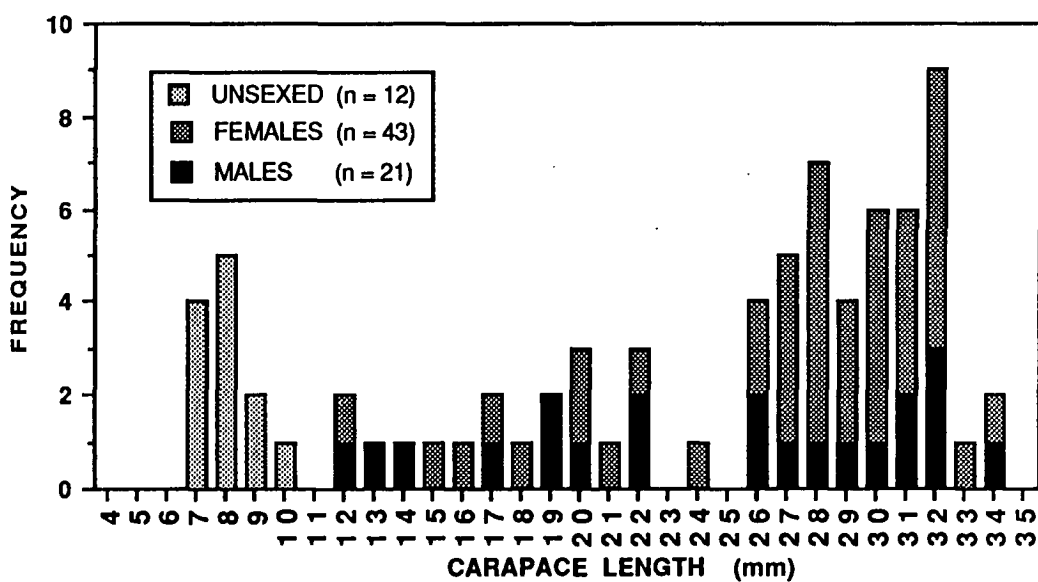
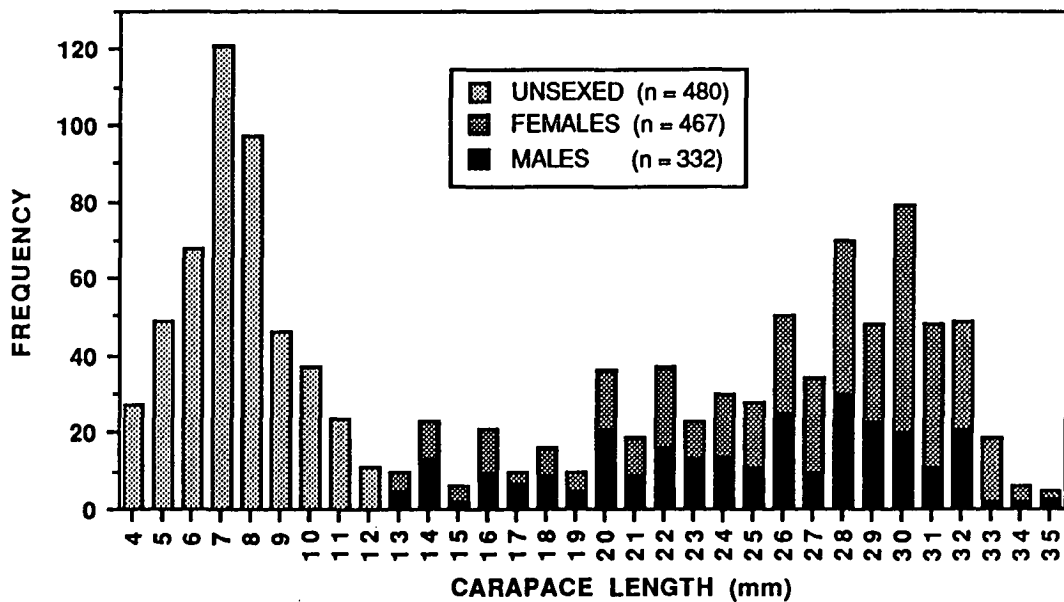


Figure 8.9 The size frequency distribution of *Astacopsis franklinii* (Western form) collected in January 1986 and February 1987 from Clarence Lagoon: **A.** All crayfishes; **B.** Females; **C.** Males

Figure 8.10 The size frequency distribution of *Parastacoides t. tasmanicus* (SP), collected from April 1985 to April 1987, at the Harlequin Hill plain sampling site in South-West Tasmania.

Figure 8.11 The size frequency distribution of *Parastacoides t. tasmanicus* (N), collected from October 1985 to March 1988, at the Needles Range sampling site in South-West Tasmania.

Figure 8.12 The size frequency distribution of *Parastacoides t. inermis*, collected from April 1985 to April 1987, at the Harlequin Hill plain sampling site in South-West Tasmania.



sampled, 362 (193 females and 169 males) individuals ranging in carapace length from 29 to 163 mm were captured and marked. Of these, 109 (50 males and 59 females) crayfishes ranging from 29.7 to 163 mm CPL were recaptured. The frequency of recapture of individual crayfishes ranged between 2 to 6 times for the duration of the study with most individuals being recaptured two to three times. The mean monthly recapture rate was 30.8 % (range = 0 to 69 %). The mean population size estimate (for crayfishes CPL \geq 30 mm) was 509.9 individuals (range = 253 - 1087, s.d. = 217, n = 13) and the density of crayfishes CPL \geq 30 mm was therefore calculated to be approximately 0.23 individuals per square meter of river or 1 crayfish per 1.47 meters of river.

Similarly, a population size estimate of 256 individuals (CPL range 28.5 -148 mm) was calculated for a 400 meter stretch of Big Creek resulting in a density of 1 crayfish per 1.56 meters of river or approximately 0.32 individuals per square meter.

Astacopsis franklinii (Eastern form): In Hobart and Guy Fawkes Rivulets, population sizes were difficult to estimate because of small sample sizes and very low monthly recapture rates. In addition, a relatively large portion of the catch was also preserved or transferred to the laboratory. Overall, of the 618 crayfish marked and released only 37 were subsequently recaptured. Of these, 35 were caught only twice and three were caught three times. The mean monthly recapture rate was 7.4 % (range = 0 - 20.8) at Hobart Rivulet and 6.3 % (range = 0 - 25) at Guy Fawkes Rivulet. The mean population size estimate (for crayfishes CPL \geq 20 mm) was 1385 individuals (range = 517 - 2451, s.d. = 641, n = 10) in the 500 meter section of Hobart Rivulet, and 1187 individuals (range = 457 - 2500, s.d. = 682, n = 8) in the 1 kilometer section of Guy Fawkes Rivulet. The resulting density estimates were therefore 1 crayfish per 0.36 m (or 2.8 crayfish / m²) and in Hobart Rivulet and 1 crayfish per 0.84 m (or 1.2 crayfish / m²) in Guy Fawkes Rivulet.

Parastacoides t. tasmanicus (SP): At the Harlequin Hill sampling site, population density estimates were obtained from monthly capture-recapture data from the 20 by 25 meters plot containing 246 pitfall traps. Overall 110 individuals (56 males and 52 females) ranging in carapace length from 12.9 to 35 mm were captured and marked in this area. Of these, 61 (31 males and 30 females, CPL 15.1 to 35 mm) were subsequently recaptured. The frequency of recapture of individuals ranged between 2 to 11 times for the duration of the study with most individuals being caught two to four times. The mean monthly recapture rate was 66.5 % (range = 33.3 to

100 %). The mean estimate for the total number of individuals (CPL \geq 15 mm) in this area was calculated to be 106.1 (s.d. = 69.7, range = 25.7 - 344.7, n = 21) and the average density was therefore 1 crayfish per 4.7 square meters (or 0.2 crayfish / m²)

Crayfish and burrow density was also estimated in other areas of the sampling site by counting and digging out all burrows in several random quadrats. The density of crayfish thus obtained was 1 crayfish per 0.9 to 2.5 m² (0.4 to 1.1 crayfish / m²) while the corresponding burrow density was 1 per 1.6 to 2.7 m².

B. MOULTING AND GROWTH

8.3.5 The moulting process

Moulting process in *Astacopsis* and *Parastacoides* is similar and was observed in the laboratory on numerous occasions in crayfishes of various size classes.

The following description of moulting in *A. gouldi* is the typical sequence of events observed prior to, during and after ecdysis:

- Approximately 30 to 35 days prior to moulting the crayfish begins to clean and enlarge its shelter. A large chamber, cleared of all loose material, is formed.

- About 15 to 20 days prior to moulting the crayfish begins preening and pulling at the old exoskeleton, presumably to loosen it away from the newly formed underlying exoskeleton. Soon after, all feeding activity ceases. The crayfish becomes very sluggish and spends most of its time sitting still in its shelter.

- Five to ten days prior to moulting the crayfish begins "busting". In this condition its carapace is noticeably swollen and a gap begins forming between the cephalothorax and abdomen, exposing the underlying swollen membrane.

- About two days prior to moulting parts of the old exoskeleton become markedly decalcified. The decalcification appears as light coloured areas on the carapace as well as on the chelae and is most pronounced on the posterior portions of the branchiostegites (Fig. 8.13B).

- Moulting begins when the membrane between the cephalothorax and abdomen ruptures dorsally. The carapace then lifts and separates from the new exoskeleton. The new folded up branchiostegites expose the gills being pulled out of their old casings. The difficult and slow process of pulling the chelae out of their old casings

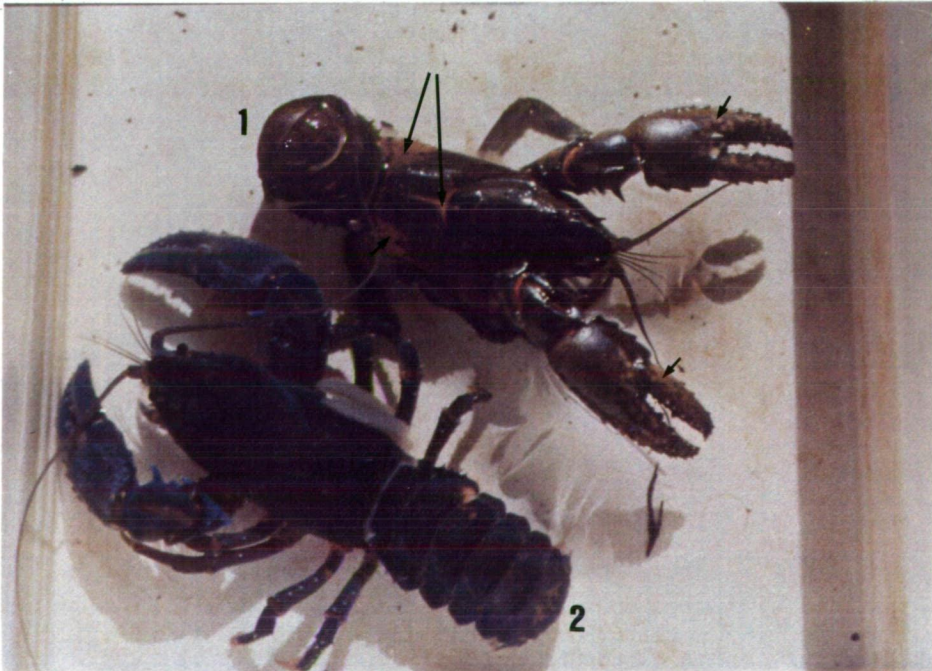
A

Figure 8.13 The moulting process in Astacopsis:

A. Crayfish emerging from exuvia.

B. The newly moulted crayfish (1) next to its exuvia (2).

Note the decalcified portions on exuvia indicated by arrows.

B

begins next, and when the palm of the chela is close to emerging, the abdomen begins to loosen from the exuvia. The chela and tail fan emerge at approximately the same time (Fig. 8.13A). The crayfish frees itself from the exuvia with a last flip of the tail. The new exoskeleton is very soft and has numerous folds and wrinkles. The entire moulting process takes approximately 35 minutes. Once free the crayfish lies on its back waving its appendages for approximately another 25 minutes. Water is absorbed at this time and the new carapace expands and becomes less wrinkled. Soon after the crayfish turns over using its thoracic appendages. Large gastroliths can be seen in the cephalic area through the new soft and thin carapace.

- Several days following the moult the crayfish is inactive while its new exoskeleton hardens. The chelae, walking legs and feeding appendages are calcified first with the rear of the carapace being last to harden.

- About 6 to 10 days after the moult the crayfish begins feeding again. The exuvia is usually partly or entirely consumed at this time and the crayfish becomes completely calcified.

8.3.6 Seasonality of moulting

Astacopsis gouldi: Data on the exact timing of moulting activity in the field was limited since most crayfishes of this species were trapped or collected while foraging. Since moulting individuals are not active only a small number of pre- or post-moult crayfish were collected. Buster and softshelled immatures (CPL 30 - 43 mm, $n = 6$) were collected in November 1986 and March 1987 while 3 freshly moulted semisoft crayfishes (CPL 77.6 mm, 80.5 mm, 81.5 mm) were collected in mid January 1986. Over the two year period, all recaptured animals of CPL 70 to 100 moulted at some time between spring and autumn. It appeared that moulting in these crayfishes occurred between November and December since mid summer and autumn captures showed that no moulting occurred in these size classes between January and June. Crayfishes of $\text{CPL} \geq 100$ also moulted during the summer months but the exact timing could not be determined.

In the animals used in the longterm laboratory growth experiments, moulting occurred from October to March in crayfishes $\text{CPL} < 40$ mm, from December to April in crayfishes $40 \text{ mm} \leq \text{CPL} \leq 60$ mm, and in March-April or October-November in crayfishes $70 \text{ mm} \leq \text{CPL} \leq 90$ mm. Three very large animals moulted in captivity:

two reproductive females CPL 131 mm and 148 mm moulted in late December and mid February respectively, while a male of CPL 167 mm moulted in late December.

***Astacopsis franklinii* (Eastern form):** The seasonal moulting cycle in adult males, adult females and immature individuals in the Mt. Wellington populations is shown in Figure 8.14. All moulting individuals were collected from deep within rock shelters in the bottom and banks of the stream. Moulting activity occurred from spring to autumn when maximum water temperatures were high, fluctuating around 15°C (see Chapter 4, Fig. 4.8). Immatures began moulting in November and moulted periodically until March-April. Gastroliths were found in immature individuals in all samples of dissected crayfish from spring to autumn. Mature males began preparing to moult in December when their gastroliths began forming and large males moulted from January to February when softshelled males were collected. Smaller, but reproductive sized males (CPL 30-35 mm) moulted well into March but none of the larger males moulted at this time. Reproductive females moulted from February to early March when busting and softshelled females with large gastroliths were found. In nonreproductive females (ie. those carrying broods), no gastrolith development or moulting activity occurred in the field or laboratory.

In laboratory animals, moulting occurred from November to March in immature individuals; from late January to early March in reproductive females and in January in large males.

***Parastacoides t. tasmanicus* (SP):** Figure 8.15. shows the seasonal moulting cycle in adult males, adult females and immature individuals in the Harlequin Hill population. Moulting activity occurred from spring to autumn when burrow water temperatures were at their highest (see Chapter 4, Fig. 4.12). Immatures began moulting in October when water temperatures rose sharply, and continued to moult periodically until May, when temperatures began dropping again. Gastroliths were found in immature individuals in all samples of dissected crayfish from spring to autumn. Mature males began preparing to moult in September when 30 % of adult males collected, showed some gastrolith formation. Males moulted from October to November when softshells and busters were collected. In December all large males were recently moulted with very clean, semi-soft exoskeletons. Reproducing females began preparing to moult in January when gastroliths began forming in 56.8% of females collected. By February, 46 % of reproductive females collected, were noted to have medium to large gastroliths. Reproductive females

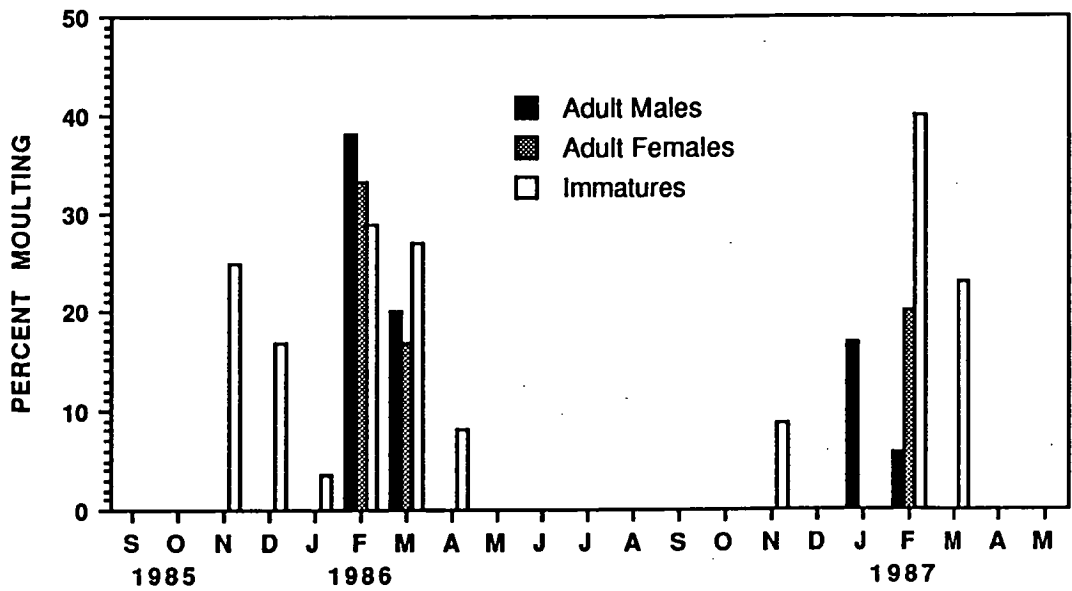


Figure 8.14 Seasonal moulting activity in *Astacopsis franklinii* from September 1985 to May 1987. (Data pooled for Hobart and Guy Fawkes rivulets.)

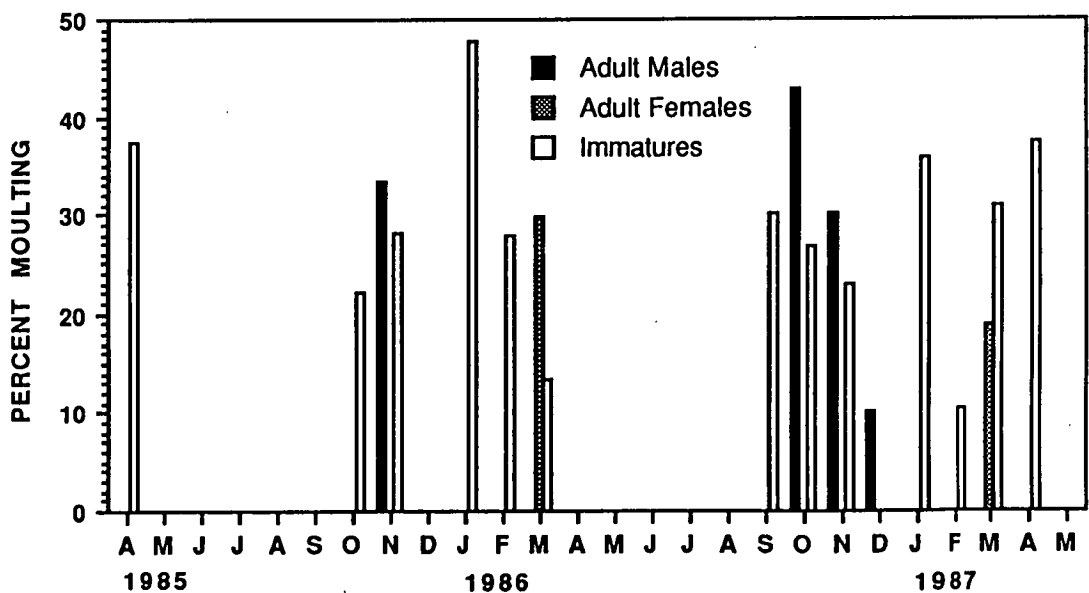


Figure 8.15 Seasonal moulting activity in *Parastacoides t. tasmanicus* at the Harlequin Hill sampling site from April 1985 to May 1987.

moulted from late February to early March when busting and softshelled females with very large gastroliths were found. Moulting closely preceded mating and spawning. No gastrolith development or moulting activity occurred at any time in nonreproductive females (ie. those carrying broods at the start of the summer).

8.3.7 Moulting increment and frequency

Astacopsis gouldi: Data on moulting increment and frequency were obtained from recaptures of marked individuals as well as from observations of animals kept in the laboratory. Of the 109 individuals recaptured, 66 (60.6 %) moulting. Of these, 28 were males and 38 were females. Only 7 individuals (5 females and 2 males, CPL 64 to 93.1 mm) moulting twice during the 14 month period during which crayfish were sampled. Of the individuals which did not moulting during the regular sampling 50 % were large (CPL \geq 90 mm).

The moulting increment in *A. gouldi* increased with size but the frequency decreased as the crayfish grew larger (Fig. 8.16 and Table 8.1). The moulting increment varied between 1 mm in very small juveniles (CPL 5 to 10 mm) to 10 to 15 mm in the very large adults (CPL $>$ 100 mm). Note that in Figure 8.16 it is not clear whether the largest increment (15 mm in a male of CPL 136 mm) was attained in one or two moultings. It is assumed here that large males moulting biennially (see below), and therefore the increment was attained in one moulting.

Crayfishes smaller than 60 mm CPL moulting two or more times per summer while the larger individuals (CPL 60 to 100 mm) moulting only once per summer (Table 8.1). There was no significant difference in growth increments between the sexes ($t = 1.1$, d. f. = 57, $p < 0.27$) Adult females (CPL \geq 120 mm) moulting only once every two summers, several months before mating. This biennial moulting pattern was observed in the field (Table 8.1) as well as in two females kept in the laboratory from October 1985 to July 1987. It appears that large males may also moulting biennially as shown by their low moulting frequencies in the field. One very large male (CPL 167) kept in the laboratory from May 1985 did not moulting in the summer of 1985-86 and subsequently died during an unsuccessful moulting in December 1986. Two other large males (CPL $>$ 100 mm) kept captive over the summer of 1986-87 also did not moulting.

The longest continuous growth record obtained in this study was for a male

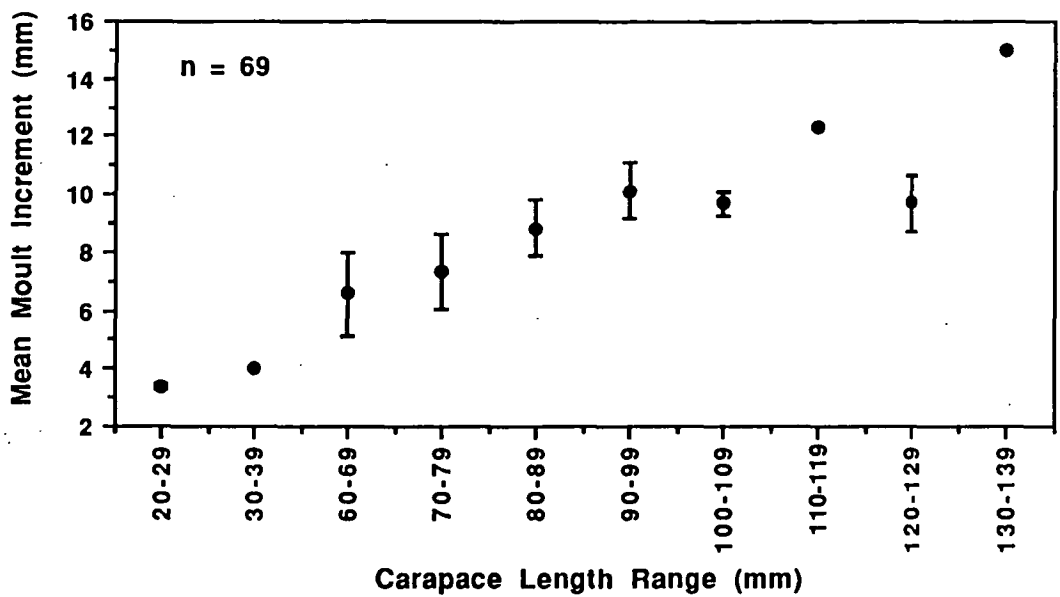


Figure 8.16 Mean moulting increment of various size classes of field captured *A. gouldi* from the Inglis River.

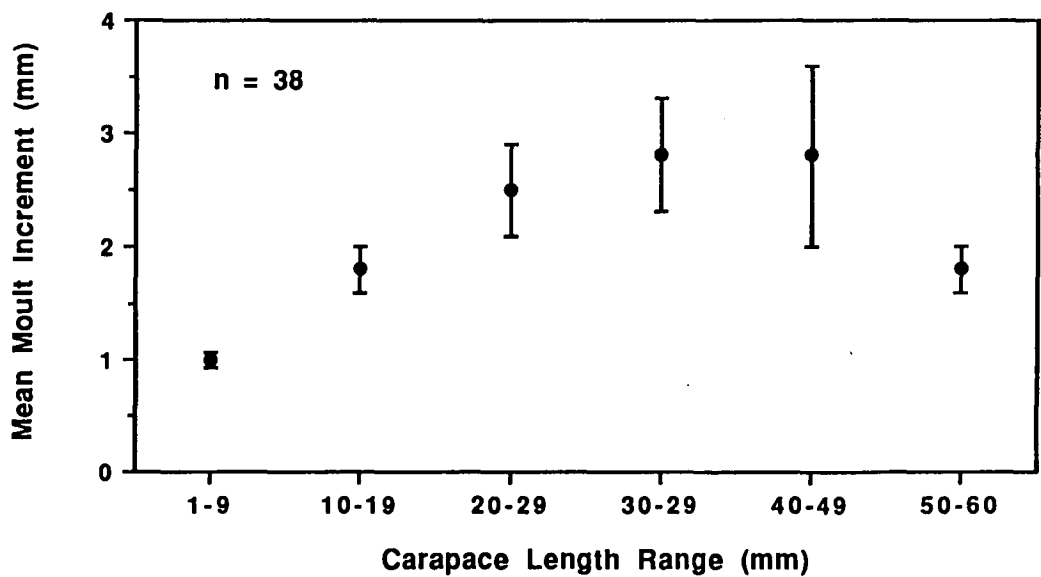


Figure 8.17 Mean moulting increment of various size classes of field captured and laboratory kept *A. franklinii* from Hobart and Guy Fawkes rivulets.

Table 8.1 Known moulting frequency in marked-recaptured *A. gouldi* of various size classes in the Inglis River between November 1985 and February 1988. (F = Female; M = Male; Numeral = number of moults; 0 = no moult; ? = unknown or no capture.)

Original Carapace Length (mm)	Nov. 85 - May 86	Nov. 86 - May 87	Nov. 87 - Feb. 88
M 55	2	?	?
F 64	?	1	1
F 68	1	1	1
F 69.5	?	1	1
F 70.3	?	1	?
F 72.5	?	1	?
F 74	1	1	1
M 76.3	?	1	1
F 79	?	1	?
F 80.3	?	1	1
M 80	1	1	?
M 81	?	1	?
F 85.5	?	1	?
F 88	1	?	1
M 89	1	1	?
F 90.2	1	?	?
F 93.1	?	1	1
M 93.2	?	1	1
M 96	?	1	?
M 107	?	1	?
M.114	?	?	1
F 119	?	0	?
F 119.6	0	1	?
F.121.6	?	0	?
M 129	0	?	?

crayfish kept in the laboratory at seasonal temperatures from 22.7.1986 to 20.10.1989. During this time, the crayfish moulted 5 times (twice in the first summer, then once each year) and grew from 57.0 mm to 93.2 mm CPL (an increase of 36.2 mm in 3 years and 3 months).

Astacopsis franklinii (Eastern form): Because of the low recapture rate in this species only limited data on moulting increment and frequency was obtained. Of the 37 animals recaptured 16 (43.2 %) moulted, and of these, 10 were males and 6 were females (initial CPL 28 - 54). Figure 8.17 shows the mean moult increments of the various size classes of crayfishes observed moulting in the field and laboratory. As in *A. gouldi*, the moult increment increased with size but then decreased somewhat in the very large adults. There was considerable variability within the increment of various size classes and no significant difference in growth increments between the sexes was found ($t = 0.58$, d. f. = 31, $p < 0.57$).

Immature crayfishes were observed moulting up to three times in one summer but the frequency may be even higher in the very small size classes. Mature females kept in the laboratory ($n = 34$) moulted only once every two summers; and, in the field, reproductive females which were about to moult still had old egg stalks attached to their pleopods suggesting that they had not undergone any moults since the release of their broods the previous summer. It is not clear whether adult males also moult biennially since none were recaptured in successive summers.

Parastacoides t. tasmanicus (SP): Of the 61 crayfishes recaptured in the pitfall traps 24 (39.3 %) moulted. Of these 9 were males and 15 were females (initial CPL 15 - 32). In addition 8 crayfishes (4 males and 4 females), ranging in CPL from 25 to 32 mm, moulted in the laboratory.

The mean moult increment of the above animals was 1.17 mm (s.d. = 0.26, $n = 7$) in immature individuals (CPL 16 to 25 mm) and 1.32 mm (s.d. = 0.40, $n = 21$) in mature individuals (CPL 26 to 32 mm).

As in *Astacopsis*, the moult frequency was higher in immature individuals and there was no significant difference in growth increments between the sexes ($t = 0.23$, d. f. = 26, $p < 0.82$). The following table shows the number of moults in marked-recaptured *P. t. tasmanicus* during the period of July 1985 to April 1987 at Harlequin Hill :

No of Moults	Mean CPL	(s.d.)	Range	n
1 Molt	29.6 mm	2.03 mm	25.7 - 32 mm	8
2 Moults	20.7 mm	5.7 mm	15.1 - 25 mm	7
3 Moults	21.7 mm	5.05 mm	15.5 - 25.3 mm	3

Mature females kept in the laboratory ($n = 34$) moulted biennially and in the field, reproductive females which were about to moult and mate still had old egg stalks attached to their pleopods suggesting that they did not undergo any moults since the release of their broods the previous summer. It appears that mature males moult once a year until they reach a carapace length of approximately 30 mm and then, like the females, begin moulting biennially. For example, one male of CPL 32 mm, which was recaptured on six occasions, moulted only once between June 1985 and December 1986.

8.3.8 Growth rate and size at age estimates

Astacopsis gouldi: The mean annual growth rate calculated on the basis of moult frequency and increment in all size classes of field marked-recaptured crayfishes was 8.4 mm (s.d. = 2.3, $n = 69$). Table 8.2 shows the calculated annual growth rates of various size classes on which the overall growth rate for the species was derived. The mean absolute growth rate of crayfishes ranging in initial CPL from 64 to 136 mm was 7.3 mm per annum (s.d. = 1.4, $n = 13$, range = 5.5 - 8.9 mm). The mean annual growth rate in laboratory kept animals was 7.4 mm (s.d. = 2.0, $n = 23$). Given such growth rates, the average age at maturity would be approximately 9 years (at 76 mm CPL) in males, and 14 years (at 119 mm CPL) in females. Since the largest specimen of *A. gouldi* measured was 214 mm CPL the life span of this species is at least 26 years.

Astacopsis franklinii (Eastern form): The size at age was difficult to estimate in this species, given the limited information on moult frequency available. Assuming that immature individuals moult as often as four times in a summer, while adult crayfishes moult only biennially, the approximate annual growth rate was calculated to be 6.8 mm (s.d. = 1.0) per summer in immature crayfishes (CPL < 45 mm) and 2.3 mm (s.d. = 0.5) per one or two summers in large, adult crayfishes.

Table 8.2 Average annual growth rates of various size classes of *Astacopsis gouldi* from the Inglis River (n = 92). Question marks indicate growth of size classes where moulting frequency could not be established with a sufficient degree of certainty.

SIZE CLASS (mm)	ANNUAL GROWTH RATE (mm)
20 - 29	7 to 10 ?
30 -39	8
40 - 49	6 -13 ?
50 -59	5 - 10
60 -69	7
70 - 79	7
80 - 89	9
90 - 99	10
100 -109	10
110 - 119	12
120 - 129	5
> 130	7.5 - 15 ?

Given such growth rates, the average age at maturity would be approximately 4 years (at 30 mm CPL) in males, and 6 years (at 46 mm CPL) in females. Since the largest specimen captured measured 61 mm CPL the maximum life span of this species is approximately 15 years.

Parastacoides t. tasmanicus (SP): The growth rate of small juveniles was estimated from size measurements of broods in their mothers burrows (Figure 8.18). After they become independent, the young remain in the female's burrow until just before the female is ready to mate and spawn again. The age of a brood can therefore be determined by examining the reproductive development of the mother. At the time the young disperse from their mothers burrow, late in the second summer of their life, they range in carapace length from 9 to 16 mm. Since the young become independent at a carapace length of 4 mm (see Chapter 7) their growth rate for this period ranges from 5 to 12 mm.

The annual growth rates of the subsequent size classes were calculated from the moult increments and frequencies of the recaptured individuals. In immature crayfishes ranging in carapace from 16 to 25 mm the annual growth increment was between 2 and 4 mm while in crayfishes of CPL \geq 26 mm it was 1 to 2 mm each summer in immatures, or every 2 summers in female and large male adults.

Given such growth rates, the average age at maturity would be approximately 3 years (at 25 mm CPL) in males, and 5 years (at 30 mm CPL) in females. Since the largest specimen captured was 35 mm CPL the life span of this species is at least 10 years.

8.4 DISCUSSION

The largest numbers of *A. gouldi* and *A. franklinii* were captured in late summer when the crayfishes were most active. This increased activity occurred during the period when water temperatures were at their highest. In other parastacids, increased catchability during late summer-early autumn has been reported in *Cherax destructor* (Lake & Sokol, 1986) and the catchability of *C. tenuimanus* was positively correlated to temperature (Morrissy, 1975). Similarly some northern hemisphere crayfishes were also found to be more active, and thus easier to capture, during summer months when water temperatures are high (Fielder, 1972;

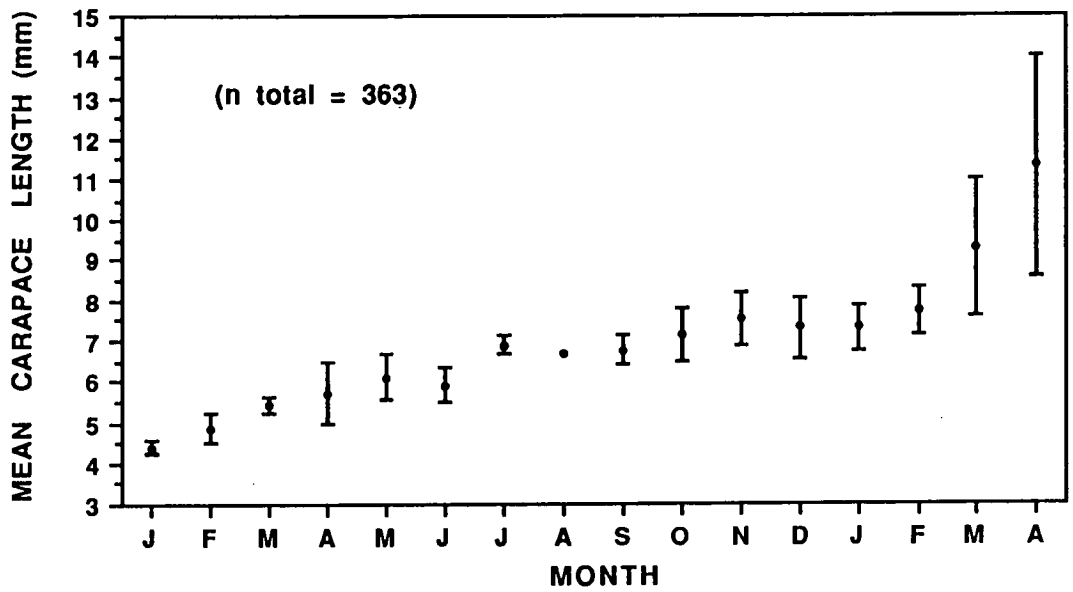


Figure 8.18 Growth of broods of juvenile *P. t. tasmanicus* from Harlequin Hill in the first 16 months of their life expressed as the mean monthly carapace length. Error bars indicate the standard deviation of the mean.

Hamr,1983; van den Brink *et al.*, 1988). In contrast, *P. t. tasmanicus* (SP) was active through the winter with the peak activity occurring in spring and autumn. The lowest levels in activity were recorded in mid summer when water temperatures was high and water levels low.

Activity patterns of both *Astacopsis* and *Parastacoides* can be explained in terms of water levels and temperature. For *Astacopsis*, which lives in a cold and swift water environment, summer temperatures represent favorable conditions with low water levels and flow, as well as warmer, but tolerable temperature. In contrast, for *Parastacoides* which lives in water-filled burrows, summer temperatures represent adverse conditions with high temperatures and very low water levels.

The sex ratio in both *A. gouldi* and *A. franklinii* was approximately 1 to 1 while in *P. t. tasmanicus* the ratio favoured females approximately by 1 to 1.3. All other *Parastacoides* subspecies also displayed this trend in sex ratios.

A 1 to 1 sex ratio, as seen in *Astacopsis*, has been shown to occur in numerous southern and northern hemisphere crayfish species (Shipway, 1951; Fielder, 1972; Eng & Daniels, 1982; Hamr,1983; Price & Payne, 1984; Lake & Sokol, 1986; Westin & Gydemo,1988; Bocic *et al.*, 1988). In contrast, a greater number of *Parastacoides* females was collected consistently throughout the year and, since crayfishes were captured by burrow excavation, this was unlikely to be the result of any sampling biases. Furthermore, Lake and Newcombe (1975) also found the sex ratio of *P. t. tasmanicus* to be 1 to 1.5 in favour of females. Woodland (1967), who found the sex ratio in *C. destructor* favoured females, proposed that females may have lower mortality because they avoid aggressive encounters. Given the biennial breeding cycle of females, a greater proportion of females would appear to be advantageous since it would result in a greater number of females breeding in a given season. On the other hand, a smaller proportion of males would be sufficient to fertilize the females, since males mature earlier and can breed each year. Additionally, males may be overall more mobile than females, and consequently may experience greater mortality due to predation or exposure to unfavourable environmental conditions. A study of the primary sex ratios in *Parastacoides* is needed to establish whether the basis for a ratio favouring females is genetic.

The polymodal frequency distributions of *Astacopsis* were typical of slow growing, long lived crayfishes being made up of large number of overlapping size classes. In both forms of *A. franklinii* there were large numbers successive size

classes of breeding adults. The considerably lower numbers of large adults of *A. gouldi* appear to be the result of overfishing in some populations (eg. Inglis River) but one would also expect their densities to be somewhat lower because of their unusually large size. However, when the size distributions of adult *A. gouldi* are compared to those of other large, unfished species such as *Euastacus hystricosus*, the adult proportions are still very low (Kehl, 1986, pers. comm.). Further research should concentrate on finding and establishing the size compositions and densities of undisturbed populations of *A. gouldi*.

In *P. t. tasmanicus* the population consisted large numbers of young of the year juveniles (CPL 6-9) mm, moderate numbers of larger immature individuals (CPL 10-20 mm) and large numbers of slow growing adults made up of numerous size classes. This suggest there is a high mortality of juveniles once they begin dispersing from their mothers burrows. This mortality can be attributed to their vulnerability to predation and competition, as well as high temperature and low water level. A similar population frequency distribution was found by Lake and Newcombe (1975) in their study of the ecology of *P. t. tasmanicus*.

The density estimates for *A. franklinii* were the highest of the three species examined (1.8-2.8 m⁻²). In *P. t. tasmanicus* density ranged between 0.2 and 1.1 individuals per m², while in *A. gouldi* it was relatively low (0.23-0.32 / m²). Lake and Newcombe (1975) found the maximum density of *P. t. tasmanicus* was 1 animal per 0.99 m². In other parastacids, density estimates range between 0.6 and 1.2/m² in *Cherax destructor*; 0.3 and 2.2 / m² in *C. tenuimanus* (Woodland, 1967; Lake & Sokol, 1986) and 0.8 and 27.5 / m² in *Paranephrops planifrons* (Hopkins, 1966). In North America, densities of 1-21 / m² in *Cambarus* and *Orconectes* (Momot *et al.*, 1978) and 0.9-1.07 / m² in *Pacifastacus* (Hogger, 1988) have been recorded, while the european *Astacus* and *Austropotamobius* occur at densities of 0.7- 7 / m² (Hogger, 1988). The densities of *Astacopsis* and *Parastacoides* are therefore comparable to those documented for other crayfishes and the somewhat lower density in *A. gouldi* maybe a function of their large size or, in some cases, the result of overfishing of adults.

The moulting process in *Astacopsis* and *Parastacoides* is similar to that described for other freshwater crayfishes (Aiken & Waddy, 1987; Lowery, 1988).

Moulting activity in *Astacopsis* and *Parastacoides* occurred between spring and autumn when temperatures rose above 10°C and the daily photoperiod was

longest. Similarly, increased water temperature and longer photoperiod have been shown to induce moulting activity in *Astacus* and *Cambarus* (Stephens, 1955; Pratten, 1980; Westin & Gydemo, 1985; Aiken & Waddy, 1987). Juveniles of both genera moulted periodically throughout the summer but moulting activity began earlier in *P. t. tasmanicus* than in *A. franklinii*. This may be attributed to the fact that standing burrow water warms up earlier and faster in the spring than the water of a swift cool stream. In addition, stream water levels and flow are very high in early spring, making early moulting dangerous as softshelled crayfish are highly susceptible to mechanical damage. Adult males and females of *A. franklinii* moulted in mid summer (Jan.-Feb.) while in *P. t. tasmanicus* adult males moulted in spring (Oct.-Nov.) and adult females moulted in March. Moulting in males and females of *Parastacoides* is therefore separated by a longer period of time, and *Parastacoides* females also moult much closer to mating than those of *Astacopsis*. As hypothesized in Chapter 7, pheromones associated with moulting may enable males to recognize the burrows of reproductive females. Since nonreproducing females do not moult, the difference in moulting condition may help the males to distinguish between reproductive and nonreproductive females.

In both *Astacopsis* and *Parastacoides*, the moulting frequency decreased with increasing size. The increment per moult increased with size initially but then decreased again once maturity was attained. The net result of such growth patterns is that large adults, especially mature females who moult biennially, actually have the lowest annual growth rates. Lower moult frequencies in larger and particularly adult crayfishes have been documented in numerous other parastacid, astacid and cambarid crayfish species (Hopkins, 1966; Pratten, 1980; Turvey, 1980; Arrignon, 1981; Jones, 1981; Lake & Sokol, 1986; O' Connor, 1984; Aiken & Waddy, 1987; Geddes *et al.*, 1988).

Biennial moulting has not been documented in the Parastacidae to date. Fradd (1979) assumed that *Parastacoides* females moulted annually but failed to show any evidence of moulting in nonreproductive (termed non-berried, in his study) females. In fact, he found that the physiological condition of nonreproductive females was not consistent with moulting. This study shows that nonreproductive females of *Astacopsis* and *Parastacoides* do not moult after releasing their young, since a year later, females about to moult (prior to spawning) have old, dirty exoskeletons and their pleopodal setae still bear old egg stalks.

It is not clear whether males in all three species moult biennially but limited evidence shows that at least some large adult males of *P. t. tasmanicus* and *A. gouldi* may moult only once every two summers. As this study did not deal in depth with growth of the three species, further research is required to clearly establish moulting frequencies and increments in various size classes of males and females.

In a laboratory study of the aquaculture potential of *A. gouldi*, Forteath (1985) found that crayfish of CPL 30-60 mm moulted twice (spring and autumn), while those of CPL 70-100 mm moulted once (spring). He also found that large crayfish (CPL 120-170 mm) did not moult over the 12 month period of his study. His results are therefore in strong agreement with this study and support the finding that large adults moult only biennially.

The slow growth in adults of *Astacopsis* and *Parastacoides*, (particularly in females) is probably the result of cool temperatures and a relatively short time available for growth and reproduction. Slower growth rates in adults have been reported in other cold-water crayfishes such as *Paranephrops zealandicus* (Jones, 1981), *Cambarus bartoni* and *Cambarus robustus* (Hamr & Berrill, 1985) and *Austropotamobius pallipes* (Brown & Bowler, 1977). In addition, the environments these species live in are generally nutrient poor. Consequently, the period needed to acquire enough energy resources to undergo a substantial size increase during a moult may be significantly longer. The relative growth rates in juveniles and adults also generally reflect their diets and foraging activities. Juveniles can be seen foraging throughout the warmer months and their diet is varied, with a relatively high animal component (Appendix B, Grows & Richardson, 1988). Adults however, must devote a large portion of their energy stores to the development of gonads, and their diets consist mainly of items of low nutritional value. Additionally, foraging activity in females appears to be reduced during the prolonged period during which eggs are incubated.

Because the growth rates of *Astacopsis* and *Parastacoides* are slow and variable, age classes are difficult to infer from frequency distributions where size classes show considerable overlap. The best size at age estimates are therefore obtained from average annual growth rates of various size classes.

The life spans in *A. gouldi*, *A. franklinii* and *P. t. tasmanicus* are relatively long when compared to most other parastacids. Exceptions are the large, Australian mainland crayfishes of the genus *Euastacus* which can also attain a considerable size

and age. Turvey (1980) estimated the maximum age of *E. spinifer* to be 10-12 years (at CPL 110-12 mm) while O' Connor (1984), calculated the age of *E. armatus* to be 10-14 years at CPL 127 mm. The life span of the yabbie *C. destructor* has been estimated to range between 3 and 7 years (Lake and Sokol, 1986). Hopkins (1966), found the maximum age of *Paranephrops planifrons* in New Zealand was at least 4 years, while Suter (1977) estimated the life span of the burrowing *Engaeus cisternarius* in Tasmania to be 2-4 years. North American *Cambarus* and *Orconectes* have maximum life spans of 3 to 4 years (Momot *et al.*, 1978; Hamr & Berrill, 1985; Hogger, 1988) while in the European *Astacus* and *Austropotamobius*, maximum age ranges between 3 and 11 years (Hogger, 1988). *A. gouldi* is therefore not only the largest but also probably the longest lived freshwater crayfish in the world.

All three species studied attain maturity at relatively late age and large size, have long life spans and slow as well as variable growth rates. The slow and variable growth appears to be a function of cold water temperature and low nutrient diets. Once the crayfishes become mature, their growth rates are further depressed (particularly in the case of the females) as energy stores are shunted towards the production of ova and sperm.

CHAPTER 9: GENERAL DISCUSSION AND SUMMARY

9.1 GENERAL DISCUSSION

Comparison of *Astacopsis* and *Parastacoides*

As predicted in one of the original hypotheses of this study, the reproductive biology and life history traits in *A. gouldi* and *A. franklinii* were more similar than when compared to those of *P. t. tasmanicus* (Table 9.1). The differences in the reproductive cycles of the two genera were however not as marked as originally expected. It was predicted that differences would occur because *P. t. tasmanicus* is a semi-terrestrial burrower while *Astacopsis* species are generally found in open, flowing water. Because the life histories of southern as well as northern hemisphere burrowing or "terrestrial" species have been seldom studied, it is difficult to make broad comparisons between them and their riverine counterparts. The small amount of information available seems to indicate that burrowing crayfish species have lower fecundities (Lowery, 1988), prolonged and less discrete mating seasons (Crocker and Barr, 1968) as well as prolonged brooding and parental care (Crocker and Barr, 1968; Horwitz *et al.*, 1985) when compared to riverine and lacustrine species.

Given that habitat type strongly influences life history traits (Begon *et al.* 1990, Southwood, 1988) the similarities between the reproductive cycles of the two *Astacopsis* species and *P. t. tasmanicus* may occur because although *P. t. tasmanicus* is generally burrowing in habit, it lives in flooded swamps (areas with high water table) where it excavates extensive burrow systems with large chambers filled with cool ground water. These burrow systems can therefore be thought of as small underground lakes which may be similar to riverine/lacustrine situations. Indeed, *P.t. tasmanicus* can be often found living in or at the edge of streams and lakes. Furthermore, this species lacks several of the morphological characters associated with tertiary (or Type 2 & 3) burrowers such as chela held in a vertical plane, increased setation and reduced abdomen size (Hobbs, 1974; Horwitz, 1986). It is therefore possible that morphologically and ecologically the species may be intermediate between an open water and an obligatory burrowing one. It would be

Table 9.1 Summary of life history characteristics of *A. gouldi*, *A. franklinii* (Eastern form) and *P. t. tasmanicus* (SP).

	<i>A. gouldi</i>	<i>A. franklinii</i>	<i>P. t. tasmanicus</i>
Habitat	aquatic cool	aquatic cool	semi-terrestrial cold in winter warm in summer
Burrow Type	most 1a, some 1b	most 1a, some 1b	most 2, some 1b
Main Diet			
adults	plant	plant	plant
Immatures	animal/plant	animal/plant	animal/plant
Sexual dimorphism			
A. Males	present	present	present
B. Females	present/pronounced	present/pronounced	present/moderate
Periodicity of spawning	biennial	biennial	biennial
Egg Incubation period	prolonged (May- Apr.)	prolonged (May- Apr.)	prolonged (Mar.-Jan.)
Fecundity	high to moderate	moderate	moderate to low
Larval development	3 moults, stage 3 attached	3 moults, stage 3 attached	2 moults, stage 3 independent
Female Size at maturity	very large (≥120 mm CPL)	medium (40-45 mm CPL)	small to medium (25-30 mm CPL)
Age groups	many	many	many
Sex ratio (M:F)	1:1	1:1	1:1.3-1.5
Growth rate	slow/very slow	slow	slow
Life span	very long	long	moderate to long
Moulting:			
Adults	Jan. - Feb.?	Jan. - Mar.	Oct.- Nov. (M) ; Mar.(F)
Immatures	Nov. - Mar	Nov. - Apr.	Oct. - Apr.

interesting to compare the life histories of *Astacopsis* and *Parastacoides* studied here to those of some of the unstudied truly terrestrial species of *Engaeus* which occur in northern and western Tasmania. Some of the information available suggests that the life cycles and reproductive morphology of at least some of the *Engaeus* species differs from the species studied here (Horwitz, 1986). Further studies of the life cycles of the little understood burrowing genera such as *Geocharax* and *Engaeus* are needed in order to resolve some of the questions involving terrestrial and riverine species and the influence of habitat on reproductive cycles of Tasmanian crayfishes.

The main differences in reproductive biology of *Astacopsis* and *Parastacoides* are seen in gonopore morphology, degree of sexual dimorphism in females, size/age at maturity, timing of spawning and moulting, spermatophore morphology and attachment, larval development and parental care.

Male *Parastacoides* have smaller, flexible gonopores which appear to function more efficiently in depositing the spermatophores. The spermatophore of *Parastacoides* is more compact and is firmly attached in close proximity of the female gonopores, while in *Astacopsis* it is rather large and can be more easily dislodged. Secondary sexual characters were observed in males and females of both *Astacopsis* and *Parastacoides*. In male crayfish, the larger chela size has been shown to enhance fighting and therefore competitive ability especially during the mating season (Stein, 1976; Berrill & Arsenault, 1984). The probability of frequent interactions between males, at least during the breeding season, seems likely since increased activity in males at the time of mating was observed in all three species.

In female crayfish, sexual dimorphism is primarily expressed in abdominal morphology and is associated with brooding of eggs. Female *Parastacoides* have less pronounced morphological dimorphism suggesting the mode of egg attachment may be more efficient or that there may be fewer risks resulting in egg loss in their habitats. In *Parastacoides* egg loss may be reduced as the brooding females are not subject to strong currents or abrasive substrate and do not encounter predators within the shelter of their burrows. Rather than morphological, the adaptations associated with brooding are probably physiological, ie: ova of *Parastacoides* may be more resistant to low oxygen and pH. Laboratory experiments confirm this view as captive *Parastacoides* broods showed much greater survivorship than those of both of the *Astacopsis* species. Overall, secondary sexual characters play an important role in reproduction of both *Astacopsis* and *Parastacoides* as they make successful

copulation and oviposition possible, contribute to the survival of offspring by affording greater protection to the incubating broods and may also act as cues for sex recognition.

The incubation period of eggs and young is shorter in *Parastacoides* and young are released in early to mid summer while food is abundant^{and} burrow water relatively warm and stable. This may allow the young to establish themselves and begin feeding within the burrow system prior to the warm, low oxygen and water level conditions of late summer. In *Astacopsis* on the other hand, young are released in late summer when the flow in their riverine habitats is lowest and temperatures are warm. This allows the young crayfish to avoid the dangers associated with flood events and grow rapidly before the onset of cooler autumn weather. Broods of *Parastacoides* are smaller, and moulting in females occurs close to mating, apparently facilitating the recognition of reproducing individuals by males. The young remain in the mother's burrow system for up to 14 months after they become independent and thus may enjoy greater protection from competition, predation and environmental stress. This initial cohabitation during the growout period may be important in their semi-terrestrial habitat where young crayfish must find or excavate new burrow systems under physiologically demanding environmental conditions. Detection of conspecifics may be important in burrowing crayfishes since individuals are probably less likely to encounter each other during foraging bouts.

Previous studies have also shown that crayfishes of the genus *Parastacoides* have evolved physiological and behavioural adaptations to deal with the unfavorable environmental conditions of their habitats. These adaptations include lower metabolic and heart rate, lower oxygen consumption and the ability to respire in air during periods when burrow water levels are low (Fradd, 1979; Swain *et al.*, 1987 & 1988). The above adaptations, when coupled with low winter water temperature, have been suggested to contribute to the lengthening of the reproductive cycle in this genus (Fradd, 1979). Further work comparing the life cycles and physiology of some of the other *Parastacoides* species living in different habitats (eg. *P. t. inermis* in alpine lakes and rainforest creeks as well as dry heath slopes and *P. t. tasmanicus* (I) in rivers) is required to clearly understand the influence of habitat and the evolution and function of the various physiological and behavioural adaptations within this interesting and varied genus.

Astacopsis species, particularly *A. gouldi*, are characterized by large to very

large size in adults. Similarly, several mainland Australian species (*Euastacus* sp.) attain a large adult size. Large size appears to be peculiar to Australian parastacids and with the exception of *C. tenuimanus* all of the very large species belong to the genera *Astacopsis* and *Euastacus*. The cause of this phenomenon in these two closely related genera is unclear but their large size may at least partly be related to their generally cool water habitats where they grow slowly, attain maturity late and live to a very old age. Cold temperature regimes may therefore influence maturity and maximum sizes of crayfish species. Interestingly, this relationship is demonstrated in *A. franklinii* where the overall maximum and maturity size increases in populations as one goes from the relatively warm and dry east and south east coast to the very wet and cold west and northwest parts of the island (see distribution maps and discussions of maturity size in Chapters 3 & 6).

Studies of other aquatic organisms have shown that temperature has influence on size, maturation and longevity. Temperature has been shown to regulate the size of maturity in the marine lobster *Homarus* in which high summer temperatures in shallow water habitats favor early maturity (at a carapace length of approximately of 55 mm) while in cold offshore habitats maturity occurs at much larger size (at a carapace length of up to 120 mm) (Aiken & Waddy, 1980). The potentially low productivity of the crayfishes' cold water habitats may further contribute to delayed maturity and large size. Cool, unproductive and high latitude environments have been shown to be responsible for slow growth, late maturation as well as lower yearly reproductive output in several European fish species (Mann *et al.* 1984).

Large size has also been associated with greater competitive fitness as well as resistance to predation (McMahon & Bonner, 1984). In Tasmania, and to some extent in mainland Australia, there are relatively few predators of crayfishes as compared to the northern hemisphere, where crayfish are consumed by a wide variety of animals such as raccoons, otters, mink, game fishes, amphibians, snakes, turtles and various waterbirds (Crocker and Barr, 1968). In the large parastacids, young and therefore small individuals may be initially susceptible to the few and relatively small predators (such as crows, blackfish and water rats), but once a larger size is attained the crayfish are relatively safe from predation. Large crayfish have heavily calcified exoskeletons with large spines and proportionately larger chela which should make them not only resistant to predation but also to any mechanical stress associated with foraging or competition for food or mates. It would therefore be advantageous to

delay reproduction until a safe size is reached and then partition the available energy between growth and reproduction. The fact that the largest females carry the most young seems to support this view. Prolonged adult life with multiple reproduction may then become a favourable evolutionary strategy in a cool unproductive environment with relatively low predation pressure. Since longer lived, large animals are thought to be better buffered from environmental stress and fluctuation (Greenslade, 1983), the larger size may also enable these crayfishes to more efficiently maintain constancy of body function under the potentially fluctuating conditions of their habitats. Large adults may therefore not only be safe from predation, but can also compete better for the available resources by being more efficient (ie: having increased mobility and decreased susceptibility to environmental stress such as flow and temperature fluctuation). Large size, coupled with the relatively long life span, may afford these species the increased resilience needed to counteract low nutrient availability and cool climatic conditions which appear to reduce their yearly reproductive rate (see following discussion on biennial breeding) and slow down their growth rates.

Finally, the particularly large size of *A. gouldi* may be related to its evolution within the Bass Strait region which has undergone climatic and sea level fluctuations during periods of glaciation (Horwitz, 1988b), since as previously stated large size helps organisms to better cope with environmental fluctuation. Alternately this species' large size may also in some way be related to its geographical isolation as island forms often attain larger size than their continental relatives (eg. the Komodo dragons of Indonesia, the coconut robber crab of the south pacific islands and the giant tortoises of the Galapagos)(McMahon & Bonner, 1984).

Biennial reproduction

As predicted in the original hypotheses, the reproductive strategies observed in *Astacopsis* and *Parastacoides* are markedly different to those of their mainland Australian counterparts. The biennial breeding and moulting cycle observed in females of these two Tasmanian genera has not been previously documented in the Parastacidae. Within the northern hemisphere Astacidae and Cambaridae, biennial breeding cycles have been reported only in some northern European populations of *Astacus astacus* and have been attributed to lack of energy reserves (in females) due to the short period of time available between the release of young and the onset of winter. Similarly the marine lobsters *Homarus americanus* and *H. gammarus*

spawn only every other year (Aiken & Waddy, 1980), with moulting and spawning occurring in alternate summers. Temperature is cited as an instrumental factor in the control of reproduction and moulting but the cause of this phenomenon in the lobsters is not clear.

In other marine invertebrates biennial breeding occurs in some species at polar latitudes (eg. the arrowworms *Sagitta* and *Themisto*^w) and individuals of polar species with biennial cycles tend to be larger than those of comparable forms in warmer latitudes (Giese & Pierce, 1974). McLaren (1966) showed that larger, biennially breeding arctic chaetognaths produce more gametes than annuals and suggested this increased fecundity might be selectively advantageous in polar regions where food is markedly seasonal. In mammals, biennial breeding occurs in large species such as bears, whales, elephants and camels where it is associated with prolonged gestation periods and parental care (Gunderson, 1976). Some of these species can also delay the implantation of ova in order to give birth at the right time of year (eg: end of winter in arctic animals). Other vertebrates where biennial reproduction occurs include some species of amphibians (alpine salamander), reptiles (vipers, gila monster and loggerhead turtle) and birds (condors and albatrosses). The underlying reasons for the two year cycles in these animals appear to be the length of gestation and parental care as well as the exhaustion of energy reserves in females following reproduction (Blüm, 1985).

The biennial breeding and moulting cycle in *Astacopsis* and *Parastacoides* appears to be a result of the cooler climate conditions in Tasmania, prolonged parental care (ie: brooding of eggs and young) as well as potentially low nutrient diets in adult females. It allows females time to replenish their energy reserves and allows the young to be released in mid to late summer when conditions are relatively stable and favorable. It remains to be seen whether all other Tasmanian crayfishes undergo this biennial reproductive cycle, but it is possible that some species or populations, particularly those living in the warmer north-eastern part of Tasmania may breed annually. Similarly, some mainland Australian species, particularly those living in cool, high-altitude environments of south-eastern Australia may also breed biennially (for example populations in streams of the Blue and Snowy Mountain Ranges). Further studies of the life cycles of Australian parastacids are needed in order to establish general trends in life history strategies of crayfish populations from the tropical north to the cool temperate south.

Life history theory

When the life history strategies of the three Tasmanian crayfishes studied here are compared to the *r*- and *K*- selection theory initially raised by MacArthur and Wilson (1967) it appears that the life histories of the Tasmanian crayfishes are most consistent with those of *K*- selected species, but their habitats do not show the characteristics consistent with this type of selection. *K*- selected species are characterized by delayed and multiple reproduction, large size at maturity, smaller broods, parental care and long life spans in constant and/or predictable environments (eg. tropics) while *r*- selected species are characterized by small size, short generation time, single reproduction and high fecundity in unpredictable environments (eg. temperate and subpolar regions) (Pianka, 1970). All three species studied here attain maturity at relatively late age and large size, have long life spans and slow, as well as variable, growth rates. Adults of all three species reproduce several times during their moderate to long life spans. Fecundity is low to moderate and extended parental care is represented by the prolonged period of brooding of eggs and young. In *A. gouldi*, although egg numbers are relatively high (200 - 1 300) when compared to other freshwater crayfishes, they are still very low when compared to related marine forms such as *Homarus* where fecundity ranges from 5 000 to 115 000 eggs per female (Aiken & Waddy, 1980). The somewhat higher fecundity of *A. gouldi* may also be offset by high mortality during the long time spent as immature animals. Immature crayfishes are more active, have an increased moulting frequency and thus are vulnerable to factors such as predation, environmental stress and competition for food and shelter.

In contrast to the apparently *K*- selected characters listed above, the environments of both *Astacopsis* and *Parastacoides* are generally harsh and subject to unpredictable changes (such as water temperature, level and flow, oxygen , etc.) and are therefore more characteristic of *r*-selected habitats. Such nonconformity with the *r*- and *K*- theory has been previously noted by other authors. Stearns (1977) noted that more than fifty percent of studies he examined did not conform to the *r* and *K* classification. He formulated a "stochastic" model for a fluctuating environment where two scenarios can occur: 1. when juvenile mortality fluctuates while adult mortality does not he predicts later maturity, smaller reproductive effort and fewer young; and 2. when adult mortality fluctuates while juvenile mortality does not we can predict earlier maturity, larger reproductive effort and more young.

Greenslade (1972) proposed another type of selection which acts in predictably unfavorable habitats, which he termed A-selection. The characteristics of species typical of such habitats include long life, late maturity, low fecundity, low rate of increase and high tolerance of environmental stress. The key factors in A-selection are given as mortality at all stages, and variation in fecundity and development rates. The relatively harsh habitats of *Astacopsis* and *Parastacoides* are similar to those described in A-selection but again not all of the expected attributes apply to their life cycles (eg. mortality of all stages, low investment in defense, low degree of specialization and high selection for parthenogenesis). The stochastic model is perhaps the best suited to the life histories described here since the environments of the species in this study are indeed fluctuating, and adult survival appears to be steady while that of juveniles probably fluctuates due to predation and environmental stress. The ongoing problem of fitting actual life history strategies to various models is perhaps still best summarized by Stearns (1977) who concluded that "we do not yet have a general and reliable theory of life history".

In conclusion, the life cycles of *Astacopsis* and *Parastacoides* are generally characteristic of the life histories shown by organisms living in high latitude, cold, unproductive and unpredictable environments. The three Tasmanian species studied here have a markedly prolonged breeding cycle, a long generation time, mature at a relatively large size and age, and produce a generally small number of large yolky eggs. Growth takes place only during months when temperatures are relatively warm and growth rates are slow as well as variable. The reproductive cycle is prolonged (biennial) and highly synchronous, with fertilization and spawning occurring in autumn, apparently in response to lowering water temperatures and decreasing photoperiod. Young are released in the summer when conditions are optimal for growth and survival.

9.2 SUMMARY

1. The reproductive biology and life history of three Tasmanian crayfishes in the endemic genera *Astacopsis* and *Parastacoides* were studied in the field and laboratory from April 1985 to May 1987.

2. *A. gouldi* and *A. franklinii* are open water species associated with riverine and lacustrine habitats from highlands to coastal plains. The latter is found throughout Tasmania while the former is restricted to the northern portion of the island. The burrowing, semi-terrestrial *P. tasmanicus* occurs in wet heathlands, water courses and highland lakes in the wetter, cooler, western half of the state. It constructs large and complex burrow networks connected to permanent water bodies and/or the water table.

3. Two distinct forms of *A. franklinii* were recognized in this study. These forms ("Western" and "Eastern") were found to differ in terms of their general morphology, reproductive biology and distribution. It is suggested subspecific or specific status may be warranted for the two forms.

4. The three species were studied in representative, relatively undisturbed habitats. The habitats of all three species were typified by low water temperatures, high rainfall and fluctuating water levels.

5. The position in the body cavity of male and female reproductive organs of *Astacopsis* and *Parastacoides* was similar to that observed in other Astacidea. The ovaries of *Astacopsis* and *Parastacoides* are similar in their basic structure consisting of a pair of sac-like lobes connected by a single commissure. The testes of *Astacopsis* and *Parastacoides* consist of two cylindrical lobes joined anteriorly by a small transverse commissure. The roughly H shaped parastacid gonads are most similar in anatomy to those of the Nephropidae and Palinuridae.. This is in contrast to the Y shaped testes of the Astacidae and Cambaridae.

6. Although superficially simple genital structures, the parastacid gonopores show considerable complexity and variation among genera. This variation is marked in the males where the gonopores consist of a raised genital papillae on the ventral surfaces of the coxae of the fifth pereiopods. The female gonopores are a pair of oval openings on the ventral surfaces of the coxae of the third pereiopods. Female

genitalia undergo significant changes at the onset of sexual maturity. These changes consist of increased setation around the gonopore as well as the decalcification of the gonopore cover. In *Astacopsis* the setal cover is lost and regained through a moult during the two year reproductive cycle of mature females.

7. Sexual dimorphism is developed to a greater degree in *Astacopsis* than in *Parastacoides*. Secondary sexual characters are more numerous in females of both genera and perform important functions in spawning and incubation of eggs. Females show sexual dimorphism by the presence of glair glands in their abdominal sterna, pleura and pleopods, heavier abdominal setation, elongation and decalcification of uropods, presence of long filamentous oosetae on pleopods, broader and deeper abdominal pleura as well as greater total length of the abdomen. The secondary sexual characters observed in males are greater total weight and larger chelae.

Secondary sexual characters are reliable indicators of sexual maturity in females of *Astacopsis* and *Parastacoides*. The complete acquisition of the full set of these characters accurately mirrors the onset of sexual maturity. Females in the process of maturing can be identified by partial acquisition of some or all of these characters.

8. Females of *A. gouldi* begin to acquire sexual characters around 107 mm CPL but do not mature fully until 119 mm CPL. The number of males examined was small but it appears that spermatophore production occurs in individuals of $\text{CPL} \geq 76$ mm.

Female *A. franklinii* (Eastern form) begin to acquire secondary sexual characters between 36 and 46 mm CPL but most do not mature until 46 mm CPL. Males apparently begin to produce sperm at approximately 30 mm CPL but 100% maturity is not reached until size classes $\geq \text{CPL } 38$ mm. The size of sexual maturity appears to be greater and more variable in *A. franklinii* Western form: females mature between 62 and 101 mm CPL while in males spermatophore production occurs in individuals of $\text{CPL} \geq 37$ mm.

Females of *P. t. tasmanicus* (SP) first begin to mature between 23 and 29 mm CPL, but the majority do not breed until 30 mm CPL. Some males apparently begin to produce sperm at approximately 16 mm CPL but 100% maturity is not reached until size classes of $\text{CPL} \geq 25$ mm. *P. t. tasmanicus* (N) and *P. t. insignis* mature at similar size to *P. t. tasmanicus* (SP) but the overall smaller *P. t. inermis* matures at a considerably smaller size ($\text{CPL} \geq 17$ mm).

9. Mature females of *A. gouldi* mate and spawn in April-May, eggs are carried over winter, hatch in January, and young stay attached until late into the following summer (March-April). After the release of their broods females overwinter, then moult in mid summer (January-February) and mate and spawn again in autumn, two years after their previous mating. Similarly, *A. franklinii* (Eastern form) mate and spawn in April-May, eggs are carried over winter, hatch in January, and young stay attached until well into the following autumn (April-May). In *P. t. tasmanicus* (SP) mature females pair with males in their burrows, moult, then mate and spawn in autumn (March - early April), carry their eggs and young until the following summer (December - January), release their broods, overwinter, then mate and spawn again the following autumn, two years after their previous mating.

Mature females of *Astacopsis* and *Parastacoides* exhibit a biennial breeding and moulting cycle. This strategy results in two distinct female reproductive groups: 1. reproductive, or those moulting, mating and spawning in a given summer and, 2. nonreproductive, or those incubating young and larvae in a given summer. The gonads of reproducing females and males show synchronous cyclic development with peak development occurring just prior to the mating season.

Abdominal eggs increase in size during the period of incubation while the rate of development of eggs and young is directly influenced by water temperature. Although the development of young is abbreviated in *Parastacoides* (ie: stage 3 young are independent) the total incubation period is of similar duration in *Astacopsis*.

10. The number of abdominal eggs as well as young was positively correlated to carapace length in all species examined. The number of ovarian eggs was not strongly correlated to carapace length in *Astacopsis franklinii* and *Parastacoides tasmanicus*. Ovarian egg counts were higher initially in early development when ova were small and yolkless, but decreased as the ovaries ripened and ova increased in size.

11. The mating behavior, the gross morphology and placement of the spermatophore in *Astacopsis* and *Parastacoides* was similar to that observed in other parastacids. Spermatophores of both genera consist of a clear matrix containing convoluted sperm tubes, but the morphology and location of placement of the spermatophore differs between *Astacopsis* and *Parastacoides*.

12. Spawning takes place immediately following copulation since long term

sperm storage is impossible due to the lack of sperm storage organs in females. The spermatophore is partly dissolved away during spawning and sperm is probably released as the eggs and associated fluids flow over the spermatophore. The spawning behaviour sequence in *Astacopsis* was similar to that described in other parastacids, astacids, cambarids and nephropids. When eggs are extruded, the abdomen is cupped tightly to form a well sealed brood chamber by folding of the abdominal segments.

13. The embryonic development was identical in *Astacopsis* and *Parastacoides* and corresponded to that described in other Parastacidae and Astacidae. There is a prominent change in the colour of the yolk which parallels embryonic development.

The general development sequence of young from stage 1 to stage 3 in *Astacopsis* and *Parastacoides* are similar to that described for other parastacid, astacid and cambarid crayfishes but several major differences between *Astacopsis* and other crayfishes are described. The postembryonic development in *Astacopsis* appears to be significantly different from other parastacids as well as astacids/cambarids and is considered to be primitive in having retained some of the ancestral marine larval characters. Given this new information it is proposed that freshwater crayfish larval development recapitulates the entire primitive decapod sequence of larval stages.

14. The largest numbers of *Astacopsis* species were captured in late summer when water temperatures were warmer and water flow and levels were lower. In contrast, *P. t. tasmanicus* (SP) was active through the winter with the peak activity occurring in spring and autumn while the lowest levels in activity were recorded in mid summer when water temperatures was high and water levels low.

15. The sex ratio in both *A. gouldi* and *A. franklinii* was approximately 1 to 1 while in *P. t. tasmanicus* the ratio favoured females approximately by 1 to 1.3. All other *Parastacoides* subspecies also displayed this trend.

16. The frequency distributions of *Astacopsis* were typical of slow growing, long lived crayfishes being made up of large number of overlapping size classes. In both forms of *A. franklinii* there were large numbers of successive size classes of breeding adults. In *A. gouldi*, the population is dominated by medium sized, non-breeding individuals while the numbers of large adults are considerably lower. In *P. t. tasmanicus* the population consisted large numbers of young of the year juveniles

lower number of larger immature individuals and large number of slow growing adults made up of numerous size classes.

17. The density estimates for *A. franklinii* were the highest of the three species examined (1.8-2.8 m²). In *P. t. tasmanicus* density ranged between 0.2 and 1.1 individuals per m², while in *A. gouldi* it was relatively low (0.23-0.32 / m²).

18. Moulting process in *Astacopsis* and *Parastacoides* is similar to that described for other freshwater crayfishes.

Moulting activity in *Astacopsis* and *Parastacoides* occurred between spring and autumn when temperatures rose above 10°C.

19. In both *Astacopsis* and *Parastacoides* the moulting frequency decreased with increasing size. The increment per moult increased with size initially but then decreased again, once maturity was attained. As a result the large adults, especially mature females who moult biennially, have the lowest annual growth rates. In *Parastacoides*, moulting closely preceded spawning and is thought to be instrumental in male-female recognition during the mating season.

20. The average age at maturity in *A. gouldi* is approximately 9 years in males and 14 years in females, while the maximum life span is at least 26 years. In *A. franklinii*, the average age at maturity is approximately 4 years for males, and 6 years for females and the maximum life is at least 15 years.

The average age at maturity in *P. t. tasmanicus*, is approximately 3 years in males, and 5 years in females. The largest specimen captured was 35 mm CPL, thus the maximum life span of this species is approximately 10 years.

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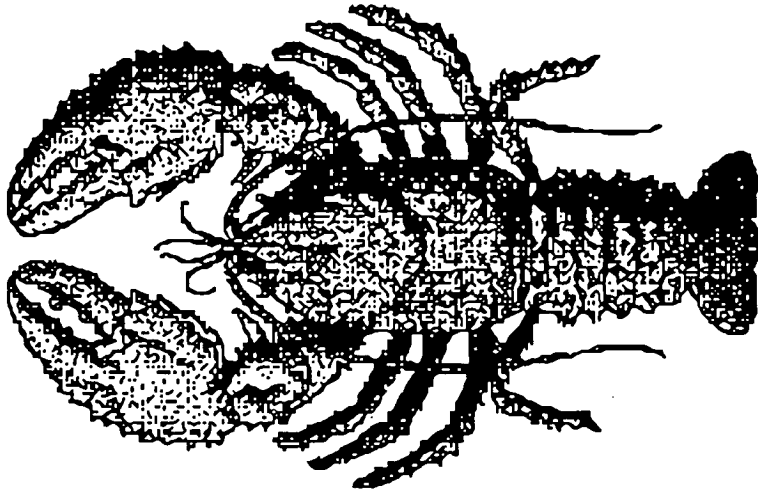
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APPENDIX A. IMPACT OF RECREATIONAL FISHERY ON *ASTACOPSIS GOULDI* POPULATIONS.

INTRODUCTION

Astacopsis gouldi, the giant freshwater crayfish or "lobster", as it is called in northern Tasmania, can attain weights of more than three kilograms and lengths in excess of half a meter (Fig A1). The species is found only in Tasmania and is restricted to the north of the state where it can be found in streams, rivers and reservoirs draining into the Bass Strait as well as in the Arthur River system in the extreme north west. The species generates worldwide interest and is the subject of regular enquiries from aquaculturalists from Australia and overseas.

The natural diet of *A. gouldi* consists of semi-decayed wood, aquatic insects, leaves and detritus (Appendix 2) but it also has a voracious appetite for animal flesh. This, together with its large size, makes fishing for this crayfish a popular pastime for inhabitants of northern Tasmania. The resulting recreational fishery is controlled by the Inland Fisheries Commission (IFC) under Tasmanian fisheries legislation. The IFC regulations state that the minimum legal size is 130 mm carapace (body) length, that females carrying eggs must never be taken and that a maximum of twelve crayfish may be taken by any one person in one day. The fishing season begins in early August and ends in late April. The use of nets and traps is prohibited. It is not clear whether a license is required to fish for *A. gouldi* but according to Dr. Pierre Horwitz's interpretation of the regulations in a recent report on the conservation status of freshwater crustacea to Australian National Parks (1989), no license is required providing a hook, rod and reel are not used. Since a baited line without a hook is the usual method employed to catch the lobster, his interpretation appears reasonable.

Figure A1

A. Shell of *Astacopsis gouldi* male from the Black River, North-West Tasmania. (CPL 207.0 mm, Collection of Inland Fisheries Commission, Tasmania).

B. Mr. Ray Wescombe holding the largest specimen captured during this study: Male, CPL: 199.5 mm, Total length: 478 mm, Locality: Dip River.



A



B

In 1969, a reserve was declared for the species at Caroline Creek near Latrobe in north west Tasmania but a recent survey of this reserve by Horwitz and Hamr (1988) showed that overfishing and poor management appear to have contributed to the decline of the population in the reserve which should thus not be regarded as a efficient conservation measure.

Recently there has been concern from scientists and fishermen over the species' status (due to overfishing and habitat alteration caused by forestry and agricultural activity) and this has led to a "vulnerable" listing in the International Union for the Conservation of Nature Invertebrate Red Data Book (Wells *et al.*, 1983). A recent study of the aquaculture potential of *A.gouldi* has found it "not a suitable animal for intensive farming" due to slow growth rates and intolerance of elevated temperature (Forteath, 1985). The author of the study, Dr. Forteath from TSIT, also pointed out that females carrying broods of young are vulnerable during the fishing season and while interviewed on the ABC television program "Countrywide" he suggested the species was declining.

METHODS

In an effort to establish the effect of recreational fishing on populations of *A. gouldi* several sites ranging from easily accessible to very remote were sampled so that population structure and frequencies of legal sized crayfishes could be compared in fished and unfished populations. Overall the following 6 additional populations were sampled from 1985 to 1988:

1. Caroline Creek: Gazetted reserve for *A.gouldi*, easily accessible and heavily poached (see Appendix 3).
2. Lilydale Falls: State reserve, popular tourist attraction, easily accessible, formerly heavily fished but presently fishing appears less intense.
3. Big Creek: similar to Inglis River sampling site, heavily fished in some areas with several more remote pools in pine plantation.

4. Detention River: On private property, relatively remote site in native forest, access restricted by "non-fishing" landowner, fishing activity relatively low.

5. Dip River: Remote site, difficult access (1.5 hours from nearest access track), fishing activity appeared relatively low.

All evidence of fishing was also carefully recorded during the regular sampling in the Inglis River. Most of this site was relatively easily accessible by forestry roads and tracks and was thus subject to fishing pressure. All old bait lines left behind by fishermen were removed so that new lines would be immediately recognized. Two pools were sampled with equal intensity at each sample to establish the number of individuals within each pool. Pool 1 was situated just upstream of a bridge where a forestry track crossed the river. It was easily accessible and showed frequent evidence of fishing activity during the second summer of sampling. Pool 2 was located further upstream and was less accessible being surrounded by relatively dense native forest. Pool 2 was about half the size of Pool 1 but did not show any evidence of fishing (in the form of old bait lines) at any time during the study.

RESULTS and DISCUSSION

Figure A2 shows the proportions of large and legal sized individuals captured at the various sites. The lowest proportions of adults occurred at the easily accessible sites (Inglis, Caroline, Big) while the highest proportion was found in the Detention River where the maximum protection was afforded because the sampling site was not only remote but access was also restricted by the land owner. Lilydale Falls is an interesting site because, although no legal crayfishes were caught, a large number of large maturing individuals were captured. This site used to be a popular fishing area (T. Hume pers. comm), but presently it is visited by a large number of tourists and therefore has become unpopular with the local fishermen. This suggest that the population may be recovering and the remaining crayfishes are growing out toward legal size. Overall however, there appears to be a direct correlation between remoteness of the sites and the percentage of legal sized crayfishes. This suggests that

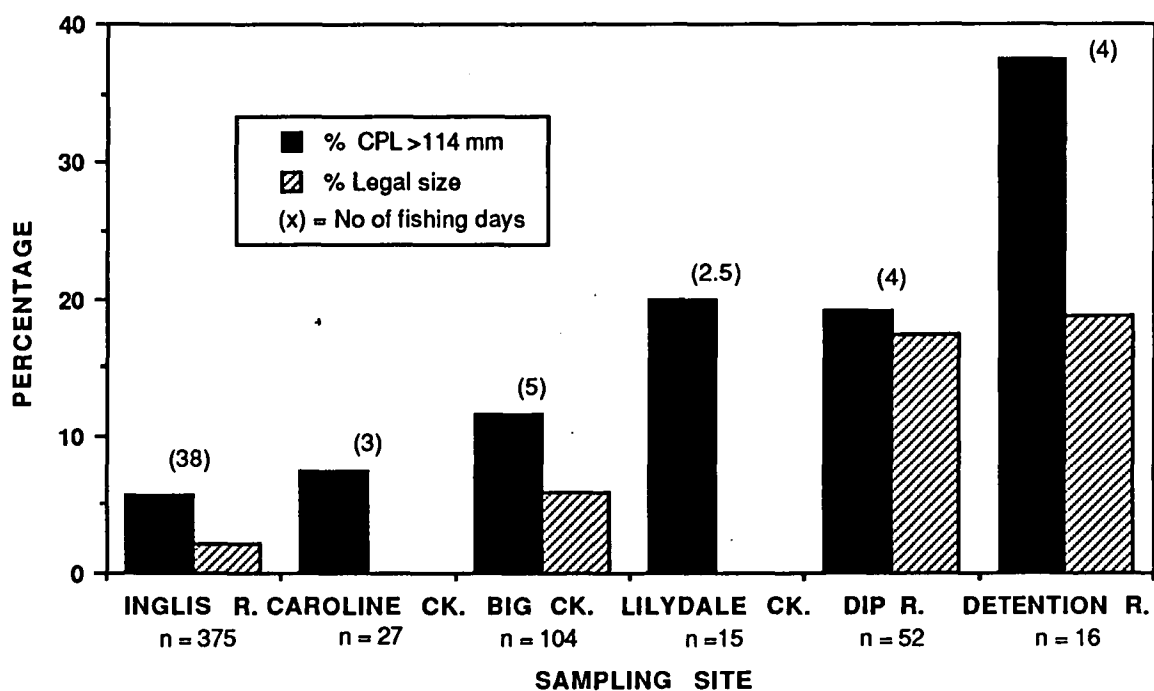


Figure A2 The percentage of large and legal sized *A. gouldi* captured at various sampling sites throughout northern Tasmania.

easily accessible sites are fished with greater intensity and this fishing pressure results in the removal of the large and thus reproducing individuals.

When the size frequency distributions of heavily fished sites are plotted (Figs. 8.5 & 8.6) there is a low number of small juveniles, relatively high number of medium sized animals followed by a sharp decrease in the number of legal sized adults when compared to the medium sized sub adults. At the unfished sites there are higher numbers of small individuals (suggesting higher recruitment) and relatively even proportions of the medium to large crayfishes. This suggests that at the fished sites, recruitment is low each year due to the low numbers of adults and, as the life span of the species is relatively long, the bulk of the population is made up of surviving medium sized (immature) individuals. Additionally, the low numbers of adults at the fished sites are in sharp contrast with the size distributions of other *Astacopsis* species where breeding adults make up large portion of the population (Figs. 8.7 to 8.9).

The results of the intensive sampling of the two pools at the Inglis River sampling site are shown in Table A1. Both pools appeared to be undisturbed in 1985-86 but in the spring of the following season new bait lines were found in Pool 1 and continued to appear through the summer until sampling ceased in May 1987. The increased fishing pressure was partly a result of widening of the track by the Forestry Commission and new access to the area via an unlocked gate on the main access road (this gate remained locked during 1985-86). As a result of the renewed fishing, the number of individuals in Pool 2 was more than halved, while in the undisturbed Pool 1 the number remained exactly the same. The number of catches was also significantly reduced in Pool 1 (χ^2 , $df = 1$, $p < 0.005$) while in Pool 2 the number of catches was not significantly different from year to year (χ^2 , $df = 1$, $p < 0.95$). In addition, only 2 (5 %) individuals were of CPL > 100 mm in Pool 1 while in Pool 2, 9 (31 %) were of CPL > 100 mm.

The results of the life history portion of this study show that the giant crayfish

Table A1 Number of captures and individuals caught in Pool 1 (fished) and Pool 2 in the Inglis River from November 1985 to May 1987.

November 1985 to May 1986			
Pool 1 (unfished)		Pool 2 (unfished)	
No. of catches	No. Individuals	No catches	No of Individuals
54	29	25	17
November 1986 to May 1987			
Pool 1 (fished)		Pool 2 (unfished)	
No. of catches	No. Individuals	No catches	No of Individuals
14	13	21	17

grows very slowly (approximately 10 mm per year), reaches maturity at a late age (8 to 15 years) and the largest specimens may be as old as thirty years. Furthermore the females reproduce only every second year thus reducing the annual reproductive potential of a given population by 50%. This study suggests that fishing is widespread and contributes to an overall decline of the large (and thus reproducing) individuals. Easily accessible sites are most affected by overfishing with the proportion of reproducing individuals dropping as low as 5% of the total population (in less accessible populations the proportion may be as high as 40%). The local fishermen claim increased incidence of poaching of egg-bearing females as well as animals below the size limit. The number of convictions made under the regulations does not reflect this trend however. In the last five years only two crayfish-related convictions have been listed by the IFC compared to over four hundred dealing with fish-related offenses.

In view of the above findings it becomes evident that the fishing regulations for freshwater crayfish are in urgent need of alteration. This study has shown that it is very difficult to catch 12 legal sized animals per day even in the densest populations. Such a large catch can damage, if not decimate, the reproductive portion of populations especially in small creeks and heavily fished accessible areas. The bag limit is therefore excessive and should be lowered from 12 to 2 or 3 animals per day per person. Given the biannual reproductive cycle and vulnerability of egg-bearing females it would be wise to ban the taking of females altogether. It is also imperative to clearly define the fishing season and enforce a strict ban on the taking of crayfish during the mating season (April to June). A clear licensing policy for crayfishing should also be instituted and the new and existing regulations should be demonstrably enforced. The present reserve at Caroline Creek is clearly inadequate due to the poor state of its population and a new reserve should be gazetted in a more appropriate location and strictly policed. One such potential location is the Gunns Plains Cave Reserve where an apparently healthy population of *A.gouldi* lives in relative safety

within the confines of the cave which is efficiently managed by the caretaker Mr. Des Wing.

It is important that an effective management programme for this species is developed if the recreational fishery is to continue since as, Momot (1984) points out, the possibility of overfishing is greater in crayfishes of higher latitudes (ie: long lived, late maturing species living in low nutrient conditions). Uncontrolled exploitation of these species results in lowering of their reproductive resilience. Large, older crayfishes are quickly harvested, reducing the brood stock and thus ultimately lowering recruitment. Such exploitation when coupled with unfavorable environmental conditions may ultimately lead to stock collapse and possible extinction.

APPENDIX B. FOOD OF *ASTACOPSIS*.

METHODS

The stomach contents of a sample of the *A. gouldi* and *A. franklinii* specimens preserved during the course of the study were examined. The stomach contents were paced in a petri dish and examined under high power with a dissecting microscope. Whenever possible, individual food items were identified and classified. The percentage of total volume of each item was scored superficially by spreading the contents over a grid placed underneath the petri dish.

RESULTS and DISCUSSION

A. gouldi : Table B1 shows the items identified in the stomachs of *A. gouldi* (n = 30, CPL 16.5 - 189.0 mm) collected from various sites between November 1986 and March 1988. Small *A. gouldi* appear to consume a greater variety of food items and the animal component of their diet is greater than that of the large adult crayfishes. The main item in the diet of large individuals appears to be decaying wood. A similar shift from animal to vegetable items, in adults, is common in many freshwater crayfish species (Goddard, 1988, Growns & Richardson, 1988). During snorkeling, large crayfishes were often seen scraping off the top layer of submerged logs. Similarly, Gould (1870) found that the stomach contents of this species consisted almost entirely of crushed and torn fragments of semi-decayed wood and concluded that submerged wood was the main source of food and that capture of animal prey by *A. gouldi* is a rarity. Despite this, the adults display a voracious appetite for animal flesh and can thus be easily attracted to baited fishing lines. It appears therefore, their mainly vegetarian diet may be a result of the lack of suitable animal prey rather than a dietary preference. The diets of the various size classes reflect the relative growth rates outlined in Chapter 8, with the smaller crayfishes having faster growth rates and more

nutrient rich diets and the large crayfishes having very slow growth rates and an apparently nutrient poor diet.

A. franklinii : Table B2 shows the items identified in the stomachs of *A. franklinii* (n = 50, CPL 24 - 61 mm) collected from Hobart and Guy Fawkes rivulets between September 1985 and May 1987. The diet of *A. franklinii* is comparable to other river and stream-dwelling freshwater crayfishes (Prins, 1968, Crocker & Barr, 1968, Hamr, 1983). A large variety of food items was consumed and the animal component was relatively high, especially in the case of the smaller crayfishes. During the summer months crayfishes were often seen foraging in the open among the leaf litter collected at the bottom of deeper pools. Several individuals were observed scraping the top layer of submerged pieces of wood with their mandibles and one crayfish (CPL 35.2 mm) was observed capturing aquatic amphipods with the tips of its large chelae. As in *A. gouldi* there was a trend for adult crayfishes to consume more vegetable matter, but various items of animal matter was still frequently found even in the stomachs of the largest crayfishes. This may be due to the fact that adults of this species are relatively small (compared to the very large *A. gouldi* adult) and can therefore still successfully capture small animal prey such as aquatic insect larvae.

Table B1 Food items found in the stomachs of *Astacopsis gouldi*.
Categories are arranged in order of relative abundance.

A. CPL < 70 mm

1. Detritus
2. Unidentified plant matter
3. Aquatic insects:
 - a. Unidentified arthropod fragments
 - b. Trichoptera larvae: Hydroptilidae, Odontoceridae, Philorheithridae
 - c. Diptera larvae: Chironomidae.
 - d. Ephemeroptera larvae
4. Crayfish exuvia
5. Gastropoda: Hydrobiidae.
6. Terrestrial insects:
 - a. Coleoptera fragments
 - b. Colembola
7. Filamentous algae
8. Nematophora: *Gordius* spp.
9. Temnocephala

B. CPL > 70 mm

1. Decayed wood fragments
2. Detritus
3. Unidentified plant matter
4. Unidentified insect fragments
5. Nematophora: *Gordius* spp.
6. Terrestrial insects: Coleoptera

Table B2 Food items found in the stomachs of *Astacopsis franklinii* (Eastern form). Categories are arranged in order of relative abundance.

1. Detritus
2. Aquatic insects:
 - a. Unidentified arthropod fragments
 - b. Trichoptera larvae: Leptoceridae, Glossosomatidae.
 - c. Ephemeroptera larvae: Ephemerellidae
 - d. Plecoptera: Eustheniidae, Gripopterygidae
 - e. Diptera larvae: Chironomidae.
3. Unidentified plant matter
4. Filamentous algae
5. Oligochaeta
6. Decayed wood fragments
7. Amphipoda
8. Gastropoda (aquatic)
9. Terrestrial insects:
 - a. Coleoptera
 - b. Diptera
 - c. Hymenoptera
10. Crayfish exuvia
11. Hydracarina
12. Isopoda
13. Ostracoda